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M. B. Mostovski

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FOREWORD

The Third International Congress of Palaeoentomology, the Second International Meeting on Palaeoarthropodology and the Second World Congress on Amber and its Inclusions gathered more than 60 delegates from 19 countries under the title of "Fossils X 3" at the South African National Biodiversity Institute in Pretoria, South Africa, from 7–11 February 2005. The participants covered a broad range of topics, highlighting insect phylogeny and systematics (21 papers, 11 posters), other arthropods (4, 5), assemblages (10, 4), biodiversity (8, 1), taphonomy and trace fossils (10, 0), amber (5, 4) , and miscellaneous (5, 2).

This volume, serving as a partial Proceedings of that Congress, also embraces a wide spectrum of subjects and presents 18 refereed papers, which are grouped into three sections.

The section on **Palaeoecology and Taphonomy** comprises five articles. Two feature taphonomy and environmental reconstructions of the Lower Permian insect beds of Kansas and Oklahoma, USA, and the Upper Permian Belmont insect beds in Australia. Two other papers are dedicated to interactions between insects and plants, and the last article highlights the ecological role of phantom-midge larvae in the Eocene Lake Messel, Germany.

As always, a majority of papers falls under **Taxonomy and Phylogeny**. Ten articles contain descriptions of 3 new families, 17 new genera, and 19 new species. Nine new combinations and 56 new synonymies are proposed. The papers cover an impressive range of Palaeozoic, Mesozoic and Cainozoic groups represented by compression fossils or inclusions in fossil resins, from localities in Argentina, Botswana, Brazil, China, the Czech Republic, England, Germany, France, Lebanon, and Russia. The following higher taxa are dealt with: Araneae, Paoliida, Grylloblattida, Blattaria, Hemiptera, Mecoptera, Diptera, and Hymenoptera. One paper continues the long-standing dispute about the dawn of insect evolution, comparing aquatic and terrestrial models of insect origins.

The last section, **Amber Studies**, offers two very important contributions that provide a profound analysis of arthropod assemblages from Eocene and Cretaceous resins.

There are also three brief notes, on new insects found in the Upper Jurassic Talbragar beds in New South Wales, Australia, on the IGCP 469 international project on the Late Variscan terrestrial biotas and palaeoenvironments, and on EDNA, the world-wide fossil-insect catalogue.

An electronic version of these Proceedings is available in the on-line Library of the International Palaeoentomological Society (http://fossilinsects.net), as is the programme and abstracts of the Congress.

We take this opportunity to express our deep gratitude to the many referees whose critical scrutiny improved the original manuscripts, and to Mr L. Maphasa, Director of the Natal Museum, for his support in the course of the preparation of the Proceedings. We also thank the authors for their patience during the long period of preparation of the volume.

We are extremely grateful to the following for financial and other assistance, without which the Congress could not have taken place: University of KwaZulu-Natal (UKZN); South African National Biodiversity Institute (SANBI); Palaeo-Anthropology Scientific Trust (PAST), specially for financial assistance toward publication of this volume; United Nations Educational, Scientific and Cultural Organization (UNESCO), specially to enable attendance by delegates from Africa; Justin James Advertising; Vacutec; Tau Safaris.

We hope that publication of this volume will encourage further studies of ancient arthropods, and we shall be able to see each other and discuss cutting-edge issues at the symposium, *Insects in Palaeoenvironments*, to be held during the XXIII International Congress of Entomology (ICE 2008) in Durban, South Africa, in 2008.

D.J. Brothers
M.B. Mostovski

photo: R.J. Beckemeyer

Delegates of The Third International Congress of Palaeoentomology, the Second International Meeting on Palaeoarthropodology and the Second World Congress on Amber and its Inclusions (Fossils X 3) on the steps of the Congress venue (South African National Biodiversity Institute, Pretoria, February 7–11, 2005):
(1) D. Shcherbakov, (2) V. Blagoderov, (3) C. Nzitunga, (4) P. Selden, (5) J. Anderson, (6) A. Arillo, (7) D. Penney, (8) T. Dikow, (9) S. Hasiotis, (10) J.-E. Wohlrabe, (11) M. Solórzano Kraemer, (12) T. Wappler, (13) R. Beattie, (14) Ed Jarzembowski, (15) R. Beckemeyer, (16) R. Toms, (17) V. Kolyada, (18) S. Dowson, (19) Ch. Hoffeins, (20) W. Krzemiński, (21) E. Krzemińska, (22) M. Mostovski, (23) V. Gratshev, (24) J. Petrulevicius, (25) J. Genise, (26) V. Krassilov, (27) Th. Schlüter, (28) H. Hoffeins, (29) B. Archibald, (30) M. Gabadirwe, (31) J. Rust, (32) D. Azar, (33) A. Rasnitsyn, (34) M. Grund, (35) L. Vilhelmsen, (36) G. Davies, (37) D. Brothers, (38) M. Pickford, (39) S. Barinova, (40) J. Serafin, (41) C. Soriano, (42) E. Perkovsky, (43) A. Ponomarenko, (44) J. Ansorge, (45) A. Ansorge, (46) C. Brauckmann, (47) J. Prokop, (48) W. Zessin, (49) C. Labandeira, (50) E. Gröning, (51) S. Zessin, (52) B. Brauckmann, (53) D. Ren, (54) S. Wedmann, (55) E. Bordy, (56) V. Perrichot, (57) X. Delclòs, (58) Yu. Popov, (59) J. Szwedo.

Absent from the photo: K. Adami-Rodrigues, A. Emeljanov, M. Engel, D. Grimaldi, V. Leggitt, I. Pinto, B. Rubidge, E. Schwab.

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OBITUARY

Vadim Gennadievich GRATSHEV

(1.05.1963—17.10.2006)

Vadim passed away untimely at the peak of his scientific career, just before finishing his PhD Thesis and in the middle of numerous projects. His studies of beetles started many years ago, when he was still a student. Vadim graduated from the Moscow State Pedagogical Institute in 1987 and taught biology at a high school for three years until 1989. Then he decided to pursue academic science and joined the Laboratory of Arthropods at the Paleontological Institute at 1991, first as a Kuperwood Fellow of the Academy of Natural Sciences, and since 1994 as a full-time researcher. Weevils and dryopoids were always his main passion, although his area of interests extended far beyond that. He produced over 20 scientific papers, including an outstanding comparative study of the hind wing venation of the superfamily Curculionoidea published in co-authorship with his late supervisor Vladimir V. Zherikhin, who he always adored.

Being a keen field researcher, he participated in numerous expeditions to the Maritime Province and Sakhalin Island, Kuznetskii Alatau, Novosibirsk Region, Armenia, Azerbaijan, Georgia, Tadjikistan, Turkmenia, and Ukraine. He attended the Third Palaeoentomological Congress that was held in Pretoria, South Africa, in 2005, and afterwards he was extremely excited to go collecting around KwaZulu-Natal. The material he collected on this trip together with specimens from other museums, inspired him to commence a new project on Afrotropical Elmidae and Anthribidae, which regrettably has been left largely unfinished.

Vadim was an optimistic, cheerful multi-talented individual with subtle sense of humour, and his interests were not restricted to extinct and extant beetles. He was an expert in noble orchids, aquarium design and raising geckos, and published several papers on those topics. He was a skilful wood-carver, and his knowledge of Japanese history and literature was not amateur. His opinion on different matters was highly valued by his friends and colleagues. He always created an aura of peace and tolerance around him.

Vadim was survived by his wife Tatiana and his daughter Ksyusha. Vadim was always a man of “On” and “Giri”, and we shall remember him as a man of noble spirit.

M. Mostovski

CHRONOLOGICAL LIST OF SCIENTIFIC PUBLICATIONS BY VADIM GRATSHEV[1]

EGOROV, A.B. & GRATSHEV, V.G. 1990. A review of weevils of the genus *Bagous* Germ., 1863 (Coleoptera, Curculionidae) of the Soviet Far East and adjacent territories. *In*: *News in the taxonomy of insects of the Far East*. Vladivostok: Far Eastern Branch of USSR Academy of Sciences, pp. 32–39. (in Russian)

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[1] Abstracts or full versions of some publications are available on http://palaeoentomolog.ru/Personnel/grachev.html or http://fossilinsects.net/lib.htm. Vadim's PhD Thesis and some unfinished manuscripts are to be prepared for publication in due course.

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Pollen eaters and pollen morphology: co-evolution through the Permian and Mesozoic

V. A. Krassilov[1,2], A. P. Rasnitsyn[2,3] and **S. A. Afonin[2]**

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ABSTRACT

In each of the sequential periods of seed-plant evolution, there were "charismatic" pollen grains that fascinated generations of palynologists. In the Permian, such peculiar pollen morphologies included taeniate pollen (with the wall split into bands, or taeniae) of *Protohaploxypinus–Lunatisporites* and *Vittatina* groups. One or more types of taeniate pollen prevailed in the pollen load of several species of Permian insects. The advent of the Mesozoic era was marked by a spread of smooth asaccate pollen of "*Ginkgocycadophytus*" type, virtually indistinguishable in the dominant orders of Mesozoic gymnosperms. Such pollen was never found in the guts. Charismatic through the Mesozoic was the rimulate pollen of *Classopollis* type. It constituted a monospecific load in the guts of large Jurassic katydids (*Aboilus*, Haglidae). The *Eucommiidites* group, related to gnetophytes, is peculiar in having lateral grooves parallel to the main sulcus. Recently this pollen type has been found in the gut compression of a xyelid, genus *Ceroxyela*. The reason why Palaeozoic and Mesozoic insects showed preferences for pollen with distinctive morphologies might be that, on the basis of the surface ornamentation of these different varieties, insects were able to distinguish edible pollen types. The distinctive pollen morphologies might have evolved primarily for this purpose.

KEY WORDS: Palynology, taeniate pollen, *Classopollis*, *Eucommiidites*, Grylloblattida, Hymenoptera, Hypoperlida, Orthoptera, Palaeomanteida, Psocida, co-evolution, Permian, Mesozoic.

INTRODUCTION

Pollen preserved in gut compressions of fossil insects gives direct evidence of feeding habits that played a significant role in morphological evolution of insects since the Permian (Krassilov & Rasnitsyn 1999 and elsewhere). In particular, a recent find of pollen grains in the intestines of *Sellardsiopsis conspicua* G. Zalessky (Palaeomanteida) confirms a hypothesis of pollinivory in the ancestral group of Holometabola (Rasnitsyn 1980). Yet the question remains whether or not the impact of pollen eaters on their forage plants was reciprocated. In order to test a hypothesis of co-evolution, we take a closer look at the morphology of pollen grains that met the dietary requirements of Palaeozoic and Mesozoic insects.

Both in the Permian and Mesozoic, there are rather featureless pollen grains, a nuisance for palynotaxonomists. On the other hand, there are fewer, but prominent pollen grains, readily recognizable owing to their distinctive surface features, such as taeniae, rimulae, pseudopores, pseudosulci. *Protohaploxypinus*, *Vittatina*, *Classopollis*, *Eucommiidites*, are some of the pollen varieties which are attractive as the objects of detailed morphological classification, because, with proper microscopic techniques, they display variations of their surface microstructures that seem taxonomically significant. For this same reason, they provide good stratigraphic markers, which makes them charismatic in the eyes of palynostratigraphers. Our data on pollen load of fossil insects indicate that not only palynologists, but also pollinivorous insects were attracted by pollen grains with ornamental surface patterns.

MATERIAL AND METHODS

The material was collected from rich localities of fossil plants and insects in the Lower Permian (Kungurian) of Tschekarda, the Central Cis-Urals; the Upper Jurassic of the Karatau Range, southern Kazakhstan; and the Lower Cretaceous of Baissa, Transbaikalia (Table 1; descriptions of the localities can be found in Ponomareva *et al*. 1998; Doludenko & Orlovskaya 1976; Krassilov & Bugdaeva 1999). The insect collections have been surveyed for specimens with gut contents preserved as compressions of organic matter visually distinct against the impression of the insect body due to their different microstructure and coloration. Pollen grains discernible at low magnification were picked up with thin needles under a stereomicroscope. Alternatively, they were extracted by maceration of embedding rocks. Microsamples

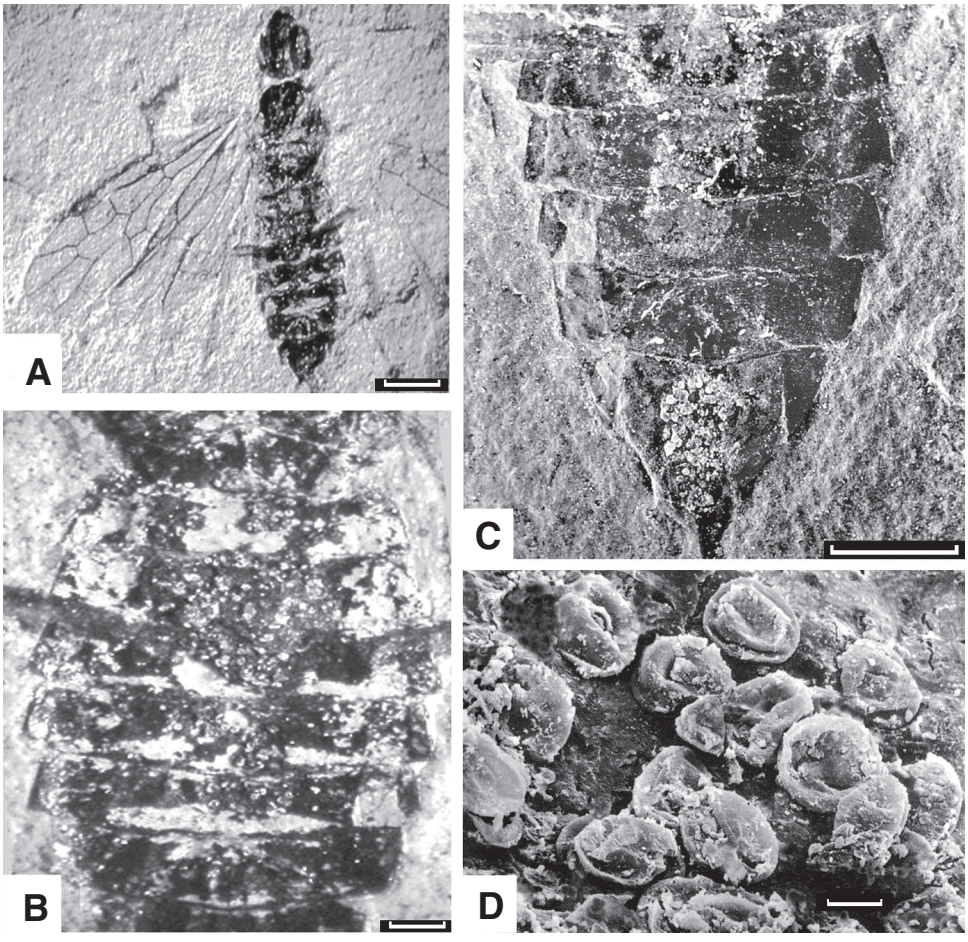

Fig. 1. *Eucommiidites* group pollen (*Cryptosaccites pabularis* Krassilov et Tekleva) in the gut compression of *Ceroxyela dolichocera* Rasnitsyn (Xyelidae, Hymenoptera) from the Lower Cretaceous of Baissa, Transbaikalia: (A) insect impression; (B) stereomicroscope view of the fore-gut with pollen grains; (C) pollen grains amassed at the hind end of the abdomen, (D) same, enlarged. Scale bars: 2 mm (A), 1 mm (B, C), 30 μm (D).

were taken at several places along the intestines to account for possible variations in the pollen load. For example, in the recently studied pollen load of *Ceroxyela dolichocera* Rasnitsyn, pollen grains are dispersed all over the intestines with the larger concentrations in the fore-gut and near the anus (Fig. 1). The pollen might have been taken at consecutive visits to the forage plant, yet no differences between the clumps have been revealed by microsampling. Pollen clumps and individual grains were mounted for light microscopy and scanning electron microscopy, as well as cut for transmission electron microscopy. Some pollen grains passed through the intestinal tract undamaged, while in other cases the external exinal layers were variously affected by digestion.

RESULTS

Pollen grains with banded (taeniate) surface structure form the most distinctive morphological group through the Permian extending to the Early Triassic. Taeniate morphologies are recorded from all parts of Laurasia as well as Gondwana, making the regional palynofloras more uniform than their contemporaneous macrofossil assemblages. Variation within the group involves configuration, density and regularity of the band patterns, providing generic distinctions (Figs 2A–D). The most common *Protohaploxypinus*-type grains with numerous uniform taeniae were produced by pteridosperms and glossopterids (Zavada 1991). *Lunatisporites*, with about four broad taeniae on the apertural face, is ascribed to the ullmannioid conifers (Balme 1995); at least some variants of a diverse *Vittatina* group with dense narrow bands associate with phylladoderms (Meyen 1987).

In the Kungurian of Tchekarda we found taeniate pollen grains in the gut compressions of *Idelopsocus* (Hypoperlida), *Parapsocidium* (Psocida), *Sojanidelia* (Grylloblattida), and *Sellardsiopsis* (Palaeomanteida, = Miomoptera). Among them, *Sellardsiopsis conspicua* was monophagous, with the pollen load consisting of *Protohaploxypinus* alone, while *Idelopsocus diradiatus* Rasnitsyn fed on both *Lunatisporites* and *Protohaploxypinus* (Rasnitsyn & Krassilov 1996*a*). *Sojanidelia floralis* Rasnitsyn was also oligophagous, with *Vittatina*-type and *Protohaploxypinus*-type taeniate grains mixed in the pollen load (Rasnitsyn & Krassilov 1996*b*). *Parapsocidium uralicum* G. Zalessky seemed to have been the only polyphagous insect, but taeniate grains constituted the major part of its diet, with a smaller contribution of discoid zonosaccate *Florinites–Cordaitina* type (Krassilov *et al*. 1999).

New groups of gymnosperms that appeared over the Permian–Triassic transition—the ginkgophytes, cycads, bennettites and czekanowskias—have produced rather uniform smooth anasulcate pollen, the ordinal affinities of which are scarcely recognizable in dispersed pollen assemblages. Despite their ubiquitous presence in the Mesozoic pollen samples and despite the fact that modern cycads are partly entomophilous, such pollen grains were never found in the guts of pollinivorous insects. The bennettitalean flower-like strobili might have been visited for nectar, but scarcely for pollen. In contrast, few Mesozoic morphotypes with distinctive surface features, such as *Classopollis* and *Eucommiidites*, were targeted by pollinivorous insects. Both rank among the most thoroughly studied charismatic types of extinct pollen morphotypes.

Plants producing *Classopollis*-type pollen are usually assigned to conifers (the Cheirolepidiaceae), although the pollen morphology is atypical for the group and is

TABLE 1. Insect fossils with the intestine pollen load preserved.

Insect taxon	n	Insect order	Locality	Age	Pollen taxon(s)	References
Permian						
Idelopsocus diradiatus Rasnitsyn	1	Hypoperlida	Tchekarda	Kungurian	*Lunatisporites*-type taeniate pollen: *Lunatisporites* sp., *Protohaploxypinus* sp., *Praecolpatites* sp. (rare)	Rasnitsyn & Krassilov 1996*a*
Parapsocidium uralicum G. Zalessky	1	Psocida	Tchekarda	Kungurian	*Protohaploxypinus*-type taeniate pollen: *Lunatisporites* sp. (dominant), *Protohaploxypinus perfecta* (Naumova) Samoilovich (subordinate), *Florinites luberae* Samoilovich (single grain), *Potoniesporites* sp. (single grain)	Krassilov *et al*. 1999
Sellardsiopsis conspicua G. Zalessky	1	Palaeomanteida	Tchekarda	Kungurian	*Protohaploxypinus*-type taeniate pollen: *Protohaploxypinus perfecta* (Naumova) Samoilovich	This paper
Sojanidellia floralis Rasnitsyn	1	Grylloblattida	Tchekarda	Kungurian	*Lunatisporites*-type taeniate pollen: *Lunatisporites* sp. (dominant), *Vittatina* cf. *fasciolata* (Balme et Hennedy) Bharadwaj (subordinate)	Rasnitsyn & Krassilov 1996*b*
Tillyardembia antennaeplana G. Zalessky	1	Grylloblattida	Tshekarda	Kungurian	*Cladaitina* sp.	Afonin 2000
Tshekardaenigma pollinivorum Rasnitsyn	1	Insecta *incertae sedis*	Tshekarda	Kungurian	Poorly preserved taeniate pollen	Rasnitsyn & Krassilov 1996*a*

TABLE 1. Insect fossils with the intestine pollen load preserved. (Continued)

Insect taxon	n	Insect order	Locality	Age	Pollen taxon(s)	References
Jurassic						
Aboilus amplus Gorochov	1	Orthoptera	Karatau	Late Jurassic	*Classopollis*-type rimulate pollen: *Classopollis* sp.	Krassilov *et al.*, 1997
Aboilus sp. aff. *dilutus* Gorochov	1	Orthoptera	Karatau	Late Jurassic	*Classopollis*-type rimulate pollen: *Classopollis* sp.	Krassilov *et al.* 1997
Phasmomimoides minutus Gorochov	1	Phasmatida	Karatau	Late Jurassic	leaves of ?*Pagiophyllum* cf. *peregrinum* Lindl. et Hutt. with adhered pollen grains of *Classopollis* type	Krassilov & Rasnitsyn 2000
Brachyphyllophagus phasma Rasnitsyn	1	cf. Embiida	Karatau	Late Jurassic	leaves of ?*Brachyphyllum* with adhered pollen grains of *Classopollis* type	Krassilov & Rasnitsyn 2000
Brachyphyllophagus phantasus Rasnitsyn	1	cf. Embiida	Karatau	Late Jurassic	leaves of ?*Brachyphyllum* leaves with adhered pollen grains of *Classopollis* type	Krassilov & Rasnitsyn 2000
Cretaceous						
Ceroxyela dolichocera Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Eucommiidites*-group pollen: *Cryptosaccites pabularis* Krassilov et Tekleva	Krassilov *et al.* 2003
Ceroxyela dolichocera Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Vitimipollis edulis* Krassilov	Krassilov & Rasnitsyn 1982
Anthoxyela anthophaga Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Alisporites alimentosus* Krassilov	Krassilov & Rasnitsyn, 1982
Spathoxyela pinicola Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Pinuspollenites entomophilus* Krassilov	Krassilov & Rasnitsyn 1982

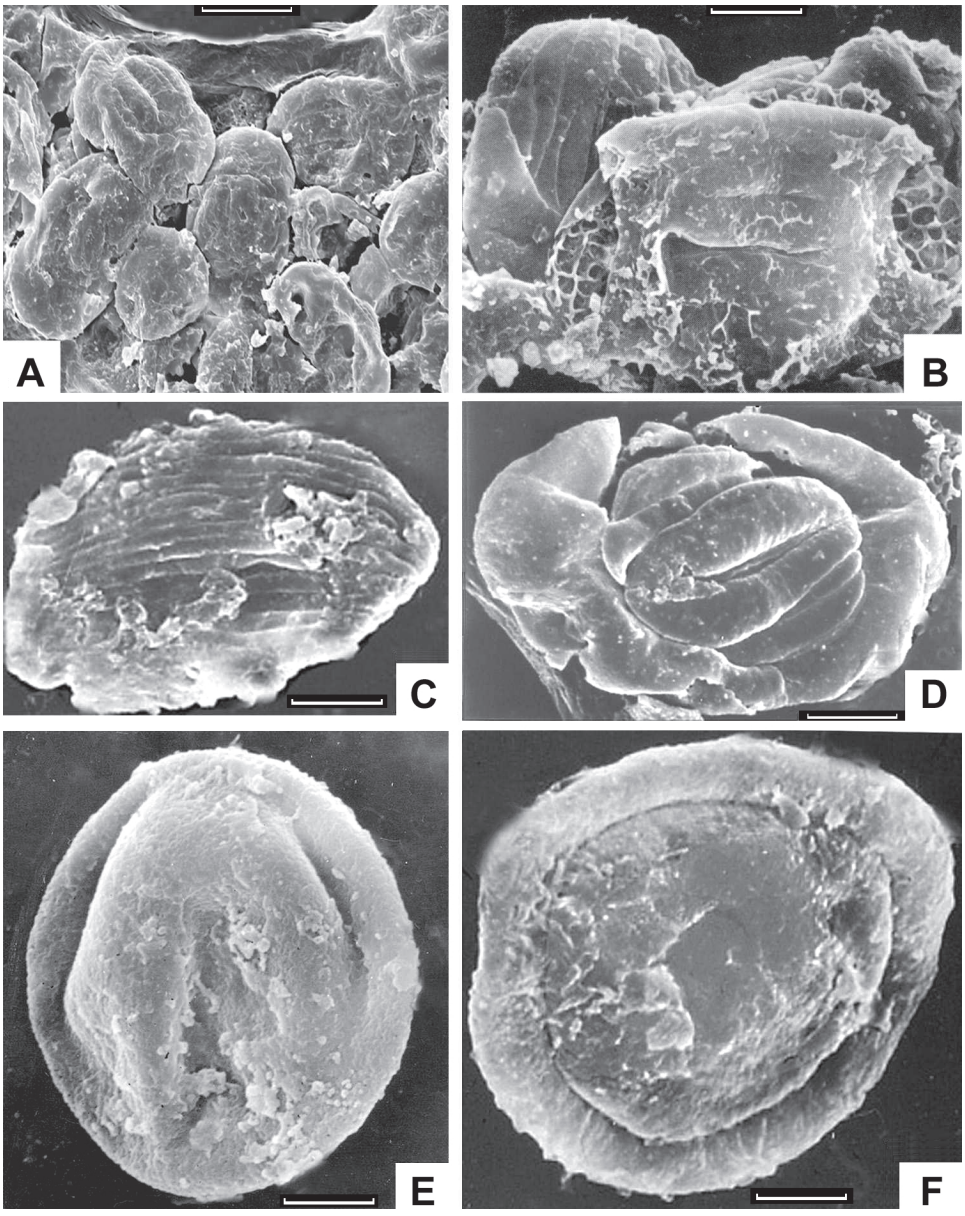

Fig. 2. Pollen loads of Palaeozoic and Mesozoic insects: (A) *Protohaploxypinus*-type taeniate pollen from *Sellardsiopsis conspicua* G. Zalessky, Lower Permian Tchekarda locality; (B) *Protohaploxypinus*-type taeniate pollen from *Parapsocidium uralicum* G. Zalessky (Psocida), same locality; (C) *Vittatina*-type taeniate pollen from *Sojanidelia floralis* Rasnitsyn (Grylloblattida), same locality; (D) *Lunatisporites*-type taeniate pollen from *Idelopsocus diradiatus* Rasnitsyn, same locality; (E) *Eucommiidites*-group pollen (*Cryptosaccites pabularis* Krassilov et Tekleva) from *Ceroxyela dolichocera* Rasnitsyn (Xyelidae, Hymenoptera), Lower Cretaceous Baissa locality, Transbaikalia; (F) *Classopollis*-type rimulate pollen from *Aboilus* cf. *dilutus* Gorochov (Orthoptera, katydids), Upper Jurassic of Karatau, Kazakhstan. Scale bars: 30 μm (A), 10 μm (B–F).

more consistent with a gnetalean affinity, suggested by Krassilov (1982) on account of ovuliferous organs. Morphologically, *Classopollis* belongs to a group of rimulate pollen with a distinctive subequatorial furrow dividing the globular grain into somewhat unequal hemispheres. The furrow is aligned with a striate equatorial ring, or cingulum, probably derived from the annular saccus of *Florinites*-like Palaeozoic predecessors. The distal hemisphere is marked by a circular pore; the proximal one, with a triangular scar revealing filaments that bound the tetraspores of a persistent tetrad.

It has been repeatedly suggested that *Classopollis*-producing plants might have been entomophilous, and our find of this type of pollen in the guts of Jurassic insects has provided additional evidence (Krassilov *et al*. 1997). In the Late Jurassic of Karatau, representatives of the grasshopper-like genus *Aboilus* (Orthoptera, katydids) were the most vigorous *Classopollis* eaters (Fig. 2F), while *Brachyphyllophagus* (Gryllones, possibly related to Embiida, the webspinners), might have consumed such pollen together with *Brachyphyllum*-type scale-leaves of the same plant (Krassilov & Rasnitsyn 2000).

Eucommiidites, with three furrows, was initially described as angiospermous, but was then found in the pollen chambers of some Jurassic and Cretaceous ovules. Therefore it appears to belong to a plant group with gymnospermous fertilization (Hughes 1961), most probably of gnetalean affinities. Yet, as was probably the case with the other charismatic pollen types, *Eucommiidites* morphology might have appeared by parallel development in different lineages of Mesozoic gymnosperms.

We studied *Eucommiidites*-type grains (though much larger than in the type species *E. troedssonii*) from gut compressions of a xyelid species, *Ceroxyela dolichocera* (Fig. 2E) from the Lower Cretaceous of Baissa locality, Transbaikalia (Krassilov *et al*. 2003). Ultrastructural studies revealed a vestigial saccus, while the lateral furrows were leptomatic, containing residual sexinal elements. *Ceroxyela dolichocera* also fed on the less distinctive saccate pollen grains produced by proangiospermous plants with monoclinous (bisexual) flowers.

DISCUSSION

We have found that Palaeozoic and Mesozoic pollinivorous insects preferred ornamented pollen grains. Some of them foraged for pollen grains with a specific surface pattern. It is well known that pollen spread by insects usually has surface structures increasing its stickiness (Faegri & Van Der Pijl 1966). However, in the case of taeniate pollen grains, *Classopollis* (with the rare exception of spinulate grains) and *Eucommiidites*, surface patterns had nothing to do with stickiness. Rather they were for visual and/or tactile perception. Although it has been repeatedly suggested that ornamented exines might have been related to arid climate, they have also been recorded from coal-bearing deposits. Moreover, the utility of taeniae, rimulae, cinguli, etc. as volume-regulated features has never been confirmed by any present-day examples.

In the Permian and early Mesozoic gymnosperms, the pollen-bearing structures were cones of peltate sporangiophores. In the absence of pollen, even an experienced morphologist would have difficulties in determining them. These organs were not distinctive enough to serve as pollen guides. At close quarters, this function was compensated by specific pollen ornamentation that might have developed and differentiated primarily for this purpose.

Several problems arising in respect to the Permian taeniate pollen morphologies—their parallel development in several gymnosperm lineages, their spread over the major phytogeographical boundaries, and their differentiation into a number of morphotypes, differing mainly in the band configuration—might have been related to pollinivory.

We hypothesise that prior to the advent of angiosperms, a mechanism of plant–insect co-evolution was at work, requiring recognition of pollen surface patterns on the part of pollinivorous insects and diversification of such patterns on the part of their forage plants. For the latter, acquisition of a recognisable surface pattern conferred the advantage of acquiring a specific pollen vector. Vicariant plant groups might have benefited in having similar pollen surface patterns when pollinated by one and the same group of insects. With the rise of angiosperms, this mechanism was replaced by recognition of flower/inflorescence patterns at a greater distance and was eventually lost.

CONCLUDING REMARKS

Spread of pollen morphologies with easily recognisable surface patterns, most conspicuously the Permian taeniate pollen grains, but also the Mesozoic *Eucommiidites* and possibly *Classopollis*, across gymnosperm lineages, is hitherto an ill-understood evolutionary phenomenon. An attempt to explain the appearance of sculptured Palaeozoic and Mesozoic pollen grains as an adaptation to arid climate failed on account of the diversity of their geographic and facial occurrences, ranging from temperate to tropical zones and from salt-bearing to coal-bearing deposits. Insofar as such pollen grains have been found in pollen loads of fossil insects, plant–insect co-evolution might have been involved in their origins. We hypothesise that, in the absence of floral cues, a visual or tactile recognition of preferable pollen (also, as one of the referees suggested, an egress of olfactory cues from taeniate pollen) played a leading role in plant–insect interaction, encouraging the development of certain types of surface structures. There must be alternative explanations, but a mere coincidence of pollen morphology and the dietary preferences in insects or a direct adaptation to climatic conditions are unlikely as candidates for such.

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Mines and galls on fossil leaves from the Late Cretaceous of southern Negev, Israel

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ABSTRACT

The recently described Late Cretaceous (Turonian) flora of Israel contains 46 species of angiosperms. Traces of galling and mining activity are exceptionally abundant and well-preserved. In a collection of more than 1000 specimens of terrestrial and aquatic angiosperms, almost all the leaves were affected. The mines consist of several morphological types, showing varying degrees of specialisation with respect to leaf histology. Some are readily identified with modern mine types; others may represent extinct types. Characters potentially useful for morphological classification of fossil mines are discussed and illustrated. Exuvial remains attributable to cecidomyiian dipterans suggest pupation in the gall, an advanced feature of this group. These findings are evidence of rapid evolution of mining and galling habits during the rise of early angiosperm-dominated communities.

KEY WORDS: Angiosperm evolution, galls, mines, palaeominology, plant-insect co-evolution, Cretaceous, Israel.

INTRODUCTION

For a long time, preservation of mine and gall traces on fossil leaves was considered an exceptionally rare phenomenon, a palaeontological curiosity. Hering (1951: 300) wrote that, although such traces deserve attention, "we cannot, however, expect from this source any new evidence on the origin of the mining habit". Owing to recent advances in the field (Labandeira *et al*. 1994; Labandeira 2002*a*, *b*) we can now speak of palaeominology and palaeocecidology, fruitful branches of palaeontological research. Fossil mines and galls provide direct evidence of the evolution of parasitic behaviour, and of plant responses to such parasitism. So preserved mines and galls are thus potentially significant since they may contribute towards a better understanding of co-evolution.

For this potential to be realised, fossil mines and galls must be studied on a regular basis. This requires a morphological classification, based on distinctive trace morphologies, such as "morphonomes" for mines and "cecidimorphs" for galls, as operational units. A few mine traces from the Late Cretaceous and Cainozoic have been named after modern genera that produce similar mines (Frič 1882; Kernbach 1967; Kozlov 1988). Morphological classification was introduced for a few Neogene galls (discussed in Brooks 1955; Strauss 1977; Waggoner & Poteet 1996).

This paper deals with certain features of fossil mines, including mine configuration with respect to leaf histology, frass deposition, consumption pattern of leaf tissue, and the succession of consecutive mine instars. These are features on which an ichnotaxonomic system of categorisation can be based. I also discuss examples of distinctive gall morphology.

The recently described Late Cretaceous (Turonian) flora of Israel (Krassilov *et al*. 2005) contains 46 species of angiosperms. The remains of terrestrial and aquatic plants occur in the Upper Shale Member of the Ora Formation, bracketed between carbonate

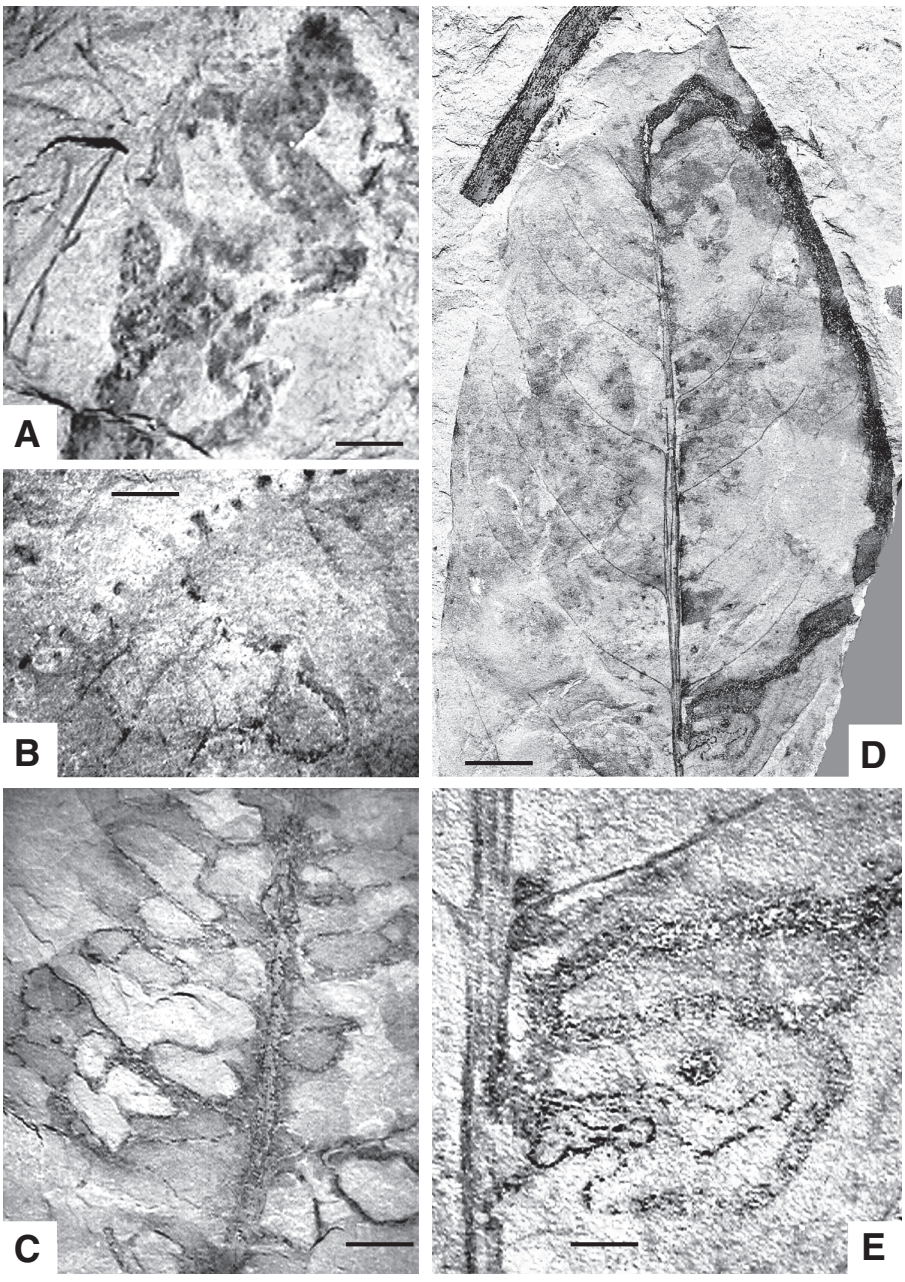

Fig. 1. Mines of Lepidoptera on Cretaceous (Turonian) leaves from the southern Negev: (A) intestiniform mine (visceronome) on *Platydebeya papilionacea*, IG1-1; (B) leaf-margin mine on *P. papilionacea* looping before the exit through a marginal gland, IG1-45; (C) two generations of blotch mines on *Dewalquea gerofitica,* IG1-644; (D) an ophiostigmatonome on *P. papilionacea*, departing between the lateral veins, arching along the margin and approaching the midrib for construction of the terminal chamber, IG1-139; (E) end-blotch of the same mine with a hibernation cocoon, frass deposited as small grains in the gallery but as slender threads in the end-blotch. Scale bars: (A) 1 mm, (B) 1.4 mm, (C) 2.7 mm, (D) 5 mm, (E) 1 mm.

sequences with mid-Turonian ammonites. The orders Ranunculales, Nymphaeales, Nelumbonales, Trochodendrales, Hamamelidales, Juglandales, Rosales, Myrtales, and Sapindales are recognised, with varying degrees of confidence, among the dicotyledons; the Najadales, Pontederiales, Arales, Cyclanthales, Arecales, and Typhales, among the monocotyledons. Modern aspects of the Turonian angiosperms from the southern Negev suggest a high rate of morphological macroevolution accompanied by ecological differentiation. Taphonomic observations have revealed that several plant assemblages are present, viz. mangroves, marshes, back-mangrove freshwater macrophytes and inland broadleaved woodland. The earliest angiosperm mangroves are inferred on the basis of taphonomic evidence, root morphology and cryptoviviparous propagules. Some flower/fruit remains indicate combretaceous and rhizophoraceous affinities of the Cretaceous mangrove species.

MATERIAL AND METHODS

Traces of mining and galling activity are exceptionally abundant and well preserved. In the collection of more than 1000 specimens of terrestrial and aquatic angiosperms, almost all the leaves are affected. The material is preserved as subcrustations or mineral films deposited beneath the cuticle, especially for epidermal mines, which are therefore even more conspicuous than in fresh leaves.

The traces were observed and photographed with a LEICA MZ6 stereomicroscope and LEICA DFC320 digital camera. The terminology for mine configuration is after Hering (1951), and for galls after Meyer (1987). The collections are deposited in the Institute of Evolution, University of Haifa, Israel, depository collection IG1.

RESULTS

Leaf Mines

About 20 distinct mine morphotypes are recognised, some of which are illustrated in Figs 1–4. The most frequently parasitised leaves are those of what is believed to be the mangrove species with supposed affinities to the Myrtales: *Paltydebeya papilionacea* Krassilov, *Eudebeya angusta* Krassilov, and *Dewalquea gerofitica* (Dobruskina) Krassilov. Leaves of extant mangroves are mined by lepidopteran caterpillars and, to a lesser extent, by Coleoptera and Hemiptera (Farnsworth & Ellison 1991). Moth attacks may even cause defoliation of mangroves (Witten & Damanik 1986), and the abundance of fossil leaves bearing lepidopteran traces may suggest similar events in the Cretaceous. *Paltydebeya papilionacea* is more vigorously attacked by miners than other species, with about 10% of leaf area lost. As in present-day mangroves (Hogarth 1999), the differences might have been due to the relative toughness of the leaf blades and their nitrogen content (C:N ratio, Feller 1995).

Fig. 1D shows a linear-blotch mine coiled at the ends (an ophiostigmatonome) starting at the midrib, running to the margin and extending parallel to it. This trajectory allowed the larva to avoid the stronger proximal parts of the lateral veins that thinned and curved distally before the margin. Several small blotches were formed along the way marking developmental shifts of the consecutive instars. The terminal portion of this mine turned back toward the midrib, a secure place to pupate, and a terminal chamber with a cocoon was formed. Frass was deposited as small pellets in the channel, but arranged in slender

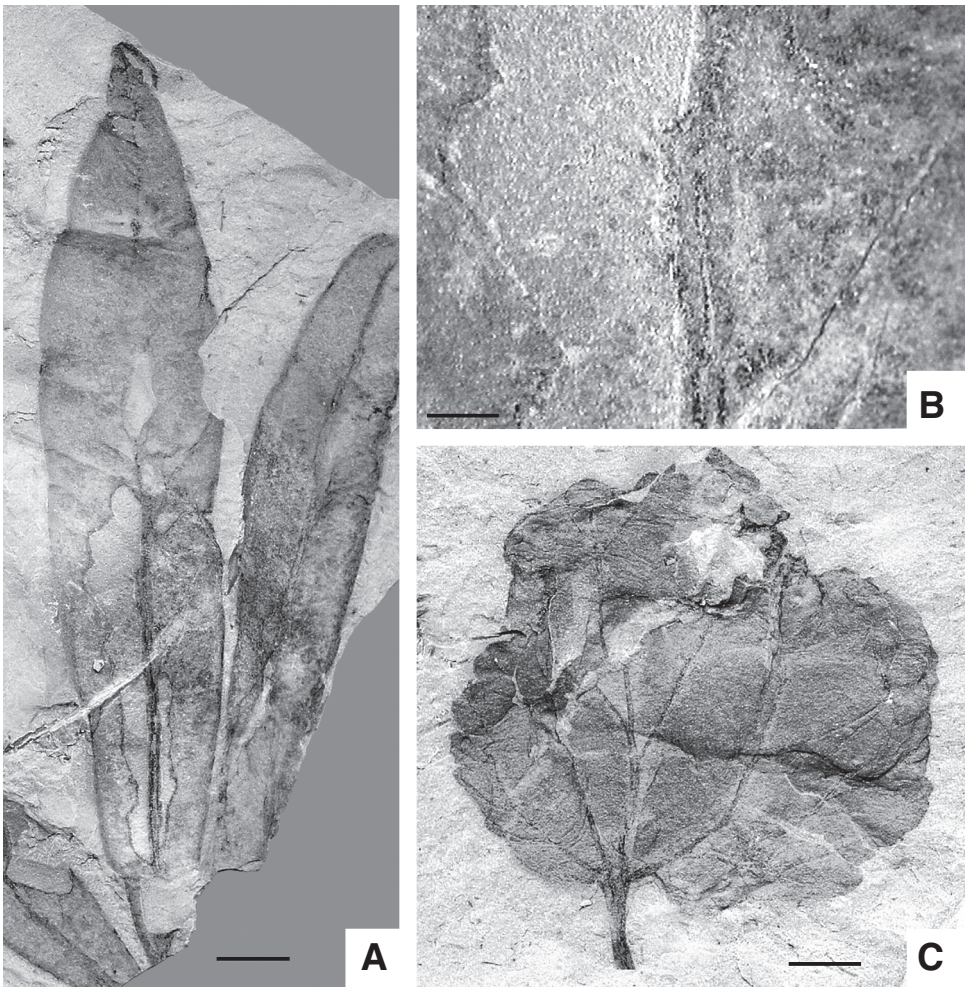

Fig. 2. (A, B) window feeding on *Dewalquea gerofitica,* IG1-847; (C) deformed leaf of *Eocercidiphyllites glandulosus* mined over the basal veins, IG1-747. Scale bars: (A) 0.3 mm, (B) 1.2 mm, (C) 0.4 mm.

threads toward the terminal chamber, reflecting a dietary change related to development of the mouthparts. The behavioural pattern of mine construction is the same as in many present-day Lepidoptera, which can be taken as evidence of a fully developed mining behaviour in mid-Cretaceous species.

Some types of blotch mines (stigmatonomes) and intestinally coiled mines (viscero-nomes: Figs 1A, 1B) find their analogues in the mines of the lepidopteran taxa *Litho-colletis* (Lyonettidae) or *Stiamella* (Nepticulidae) (Braun 1917). Marginal mines in the material are most common on the leaves with marginal glands, a source of sugar-rich sap. However, the terminal segments of such mines have deviated from the leaf margin, forming a meandering loop across the lateral veins, ending in an exit through the gland (Fig. 1B).

Examples of "epidermal windows", with all the tissues removed except the two epidermal layers (Figs 2A, 2B), suggest a feeding habit typical of coleophorid miners that spend only part of their larval life in the mine. Indeed, mines coursing along leaf margins may end in an elongate or semicircular incision, and cases built of cut-out leaf pieces are attached at or near the incision site. These leaf pieces are loosely coiled as in present-day coleophorid cases. The attachment of the cases is almost parallel to or at 45° to the leaf margin (Figs 3C–E), depending on whether the orientation of the mouth opening occurs at right angles or obliquely to the long axis of the case. Both mouth types occur in some extant lepidopteran species of *Coleophora* (Coleophoridae) (Hering 1951).

Heavily mined leaves sometimes show two generations of overlapping mines: one of relatively small elliptical dark blotches, the other of larger irregular lighter ones with meandering margins (Fig. 1C). Such differences commonly occur between successive larval instars of miners, the early one (forming small dark blotches) feeding on leaf tissues, mostly epidermis, of a higher nutritional quality than the later one, which thereby excavates larger areas and removes most of the tissue. The change of habit may suggest a seasonal hardening of leaf tissue making it less palatable. Such changes will be most pronounced during brief, dry periods which may occur between consecutive instars of miners.

A peculiar type of linear trail with two parallel-sided rows of large well-spaced frass pellets is characteristic of some dipteran (Agromyzidae?) mines. Adjacent tracks in opposite directions (retractonomes) may form very large blotches, occupying almost half of the leaf blade, but never crossing the midrib (Figs 4C, 4D)*. In other cases, tracks diverge in all directions, forming an asteronome (Figs 4A, 4B). The first type was produced by a species that oviposited approximately midway between the midrib and leaf margin, whereas the second type indicates an oviposition site on the midrib.

For leaves with palmate venation, mine trails sometimes diverge from the point of the petiole insertion and extend along primary veins. Such leaves are more or less deformed, often inequilateral and notched at the apex (Fig. 2C).

Among the aquatic plants, both aerial and floating leaves of *Nelumbites* (Nelumbonaceae, Nelumbonales) are mined, the latter showing a peculiar type of elliptical stigmatonome coarsely spun over the margins, with occasional loose stitches extending inside the loop (Figs 5A–C). No closely comparable structures have been found in any of the insect groups having mouthpart spinnerets. Lepidoptera (*Lithocolletis*) sometimes bind frass grains by spinning at the periphery of the mine, but their mining of floating leaves is unusual, whereas chironomid miners of Nymphaeaceae and Potamogetonaceae (Berg 1950) typically construct linear mines.

Galls

Galls are often found on the same leaves as mines. For example, *Dewalquea gerofitica* is infested with conical acuminate galls about 3 mm long, rather evenly spaced along the thickened margin and scattered between the lateral veins. These galls are sometimes so dense that the leaf blade is scarcely exposed at all (Figs 3A, 3B). The galls protrude

* C. Labandeira in his review of this paper has suggested that the infected area may represent damselfly oviposition. However, the arrangement of traces does not correspond to a typical pattern of zygopteran egg sets and seem more compatible with a frass-pellet interpretation. Additional material is needed to support this hypothesis.

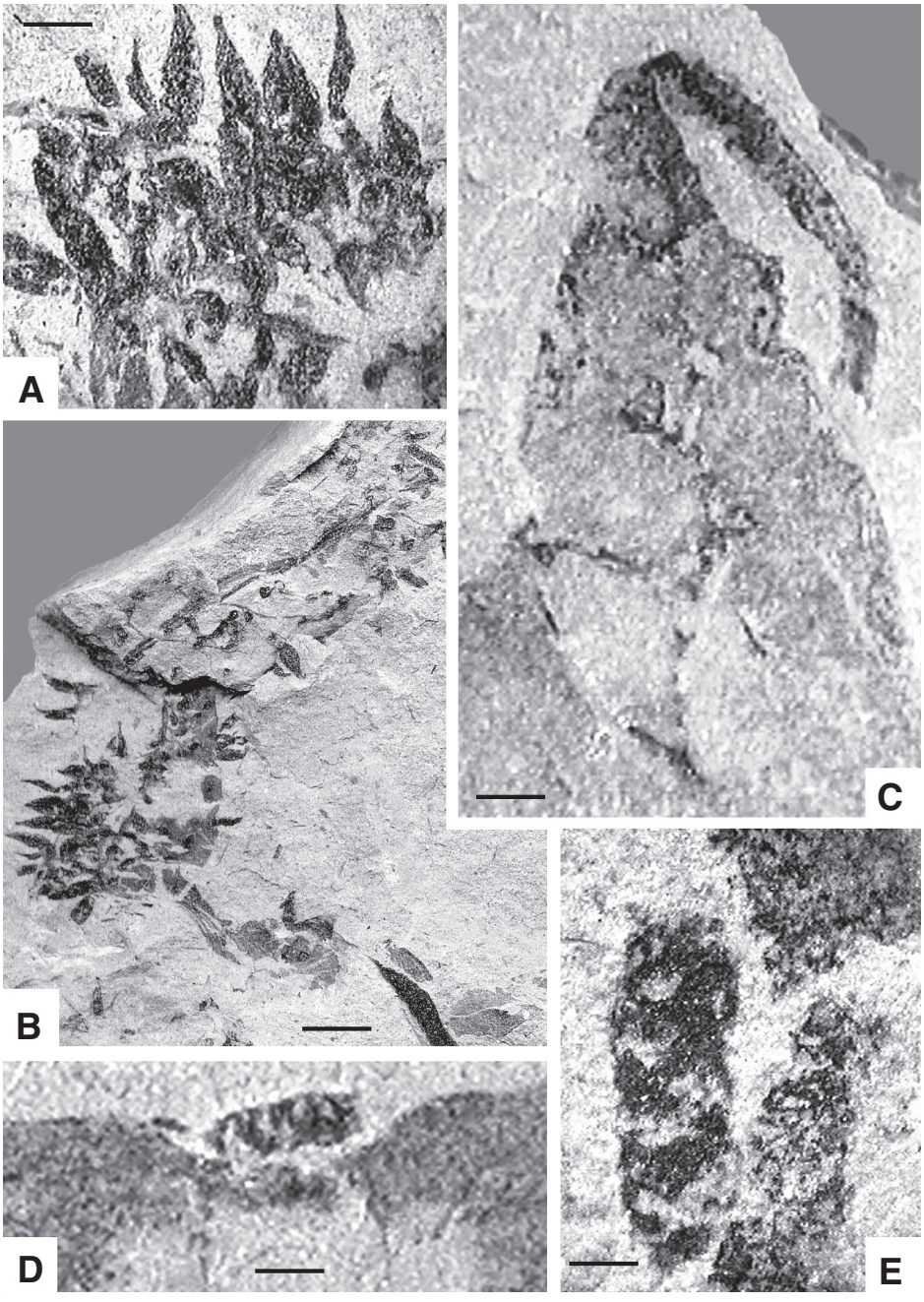

Fig. 3. Galls and larval cases on *Platydebeya papilionacea*: (A, B) leaf surface densely covered with conical galls, IG1-618; (C) tubular case attached at leaf tip almost parallel to marginal incision, IG1-191; (D, F) case of a coiled leaf piece cut out of leaf margin and attached at about 45° (classified as mouth type 3, see: Hering 1951), IG1-109. Scale bars: (A) 1.6 mm, (B) 5 mm, (C) 0.6 mm, (D) 1 mm, (E) 0.4 mm.

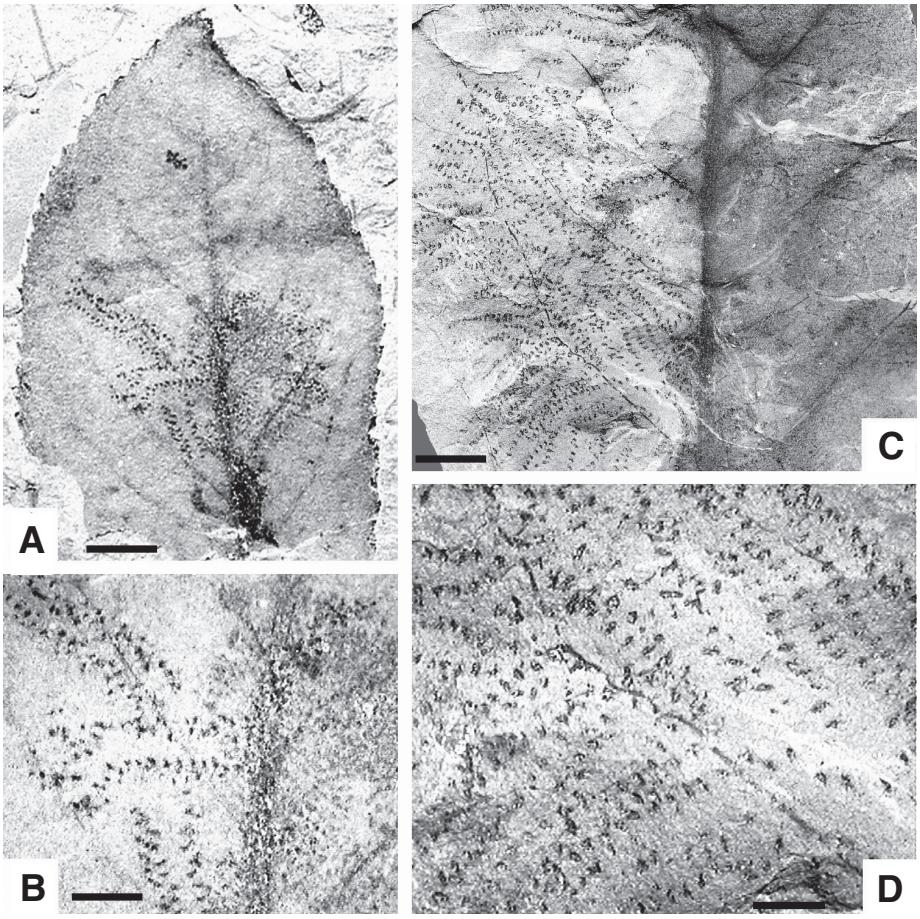

Fig. 4. Dipteran mines on *Platydebeya papilionacea*: (A, B) mine tracks with two rows of frass pellets diverging from the midrib, IG1-138; (C, D) half-blade covered with closely aligned track segments in opposite directions, with two rows of frass pellets, IG1-11. Scale bars: (A) 2.5 mm, (B) 1.2 mm, (C) 4 mm, (D) 1.3 mm.

from the upper leaf surface, opening on to the lower surface, with a disk of thickened epidermal tissue around a circular hole. An imprint of a larva preserved among the galls (arrow in Fig. 6A) shows the posterior end with five abdominal segments, while the anterior part is immersed in the growing gall.

Galls of the same type occur on *Platydebeya papilionacea*, possibly confirming its taxonomic affinities with *Dewalquea*. A detached gall (Fig. 6B) shows a neatly cut abscission area at which it was separated from the basal disk that remained on the lower side of the leaf, as in modern gall midges. Among fossil cecidia, similar structures are figured for cynipid galls on Miocene oak leaves assigned to the cecidimorph genus *Antronoides* Waggoner & Poteet, 1996 (Cynipidae, Hymenoptera) and compared to extant *Antron clavuloides* Beutenmuller (Waggoner & Poteet 1996). These galls differ from the Cretaceous cecidimorph mainly in the narrower fusiform shape and the apical bottleneck. However, the appendages emerging from the opening are here interpreted

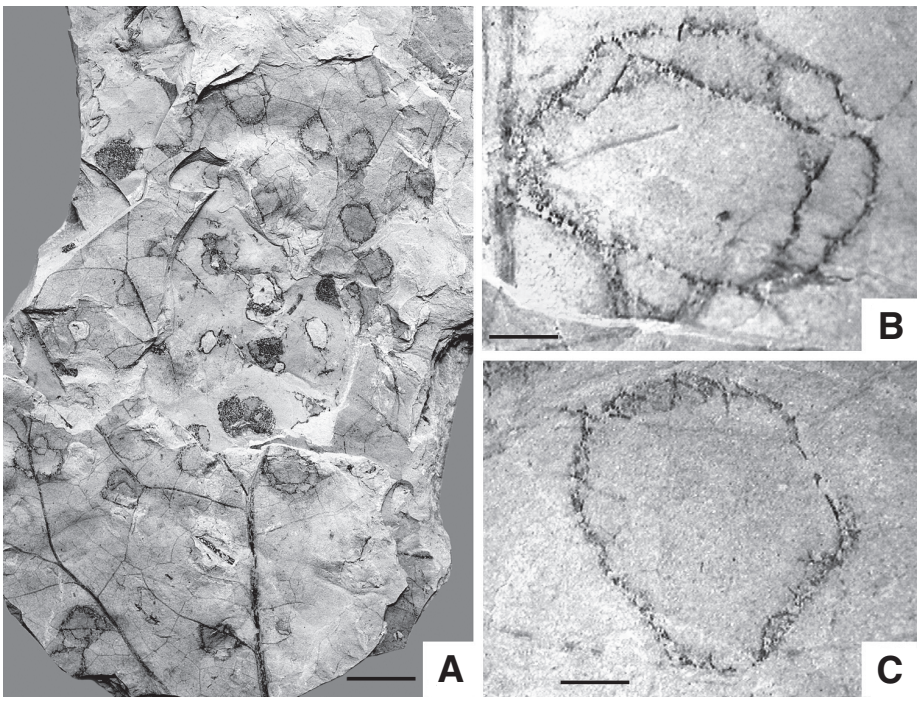

Fig. 5. Spun blotch mines on floating leaves of *Nelumbites aravensis*, IG1-11; note loose stitch in (B). Scale bars: (A) 10 mm, (B, C) 1.2 mm.

as exuvial remains of a gallicolous pupa. More specifically, antennal horns and cephalic setae are used by gall midges to cut their way out of the gall (Gagné 1994). Some fruits from the same locality resemble these types of organoid galls, suggesting a role of gall induction in angiosperm organogenesis.

DISCUSSION AND CONCLUSIONS

The feeding and habitation traces on Cretaceous angiosperm leaves from Gerofit, southern Negev, show evidence of insect groups, principally Lepidoptera and Diptera, that are not represented among the body fossils from the same locality, which consist mainly of Orthoptera and Coleoptera. The diversity of mine types in the Turonian of the Negev is much higher than in any leaf assemblage of the preceding geological ages (reviewed in Boucot 1990; Labandeira *et al*. 1994; Scott *et al*. 1994), including the Cenomanian assemblage of Lebanon (Krassilov & Bacchia 2000), which suggests explosive evolution of the mining habit. Diverse serpentine mines on platanoid leaves from the Turonian of Kazakhstan (Kozlov 1988) indicate a simultaneous increase in numbers of mining insects in other regions.

The mine types differ in the configuration of the mine track; their course with respect to the leaf margin, midrib and laterals, and frass deposition; and features related to the duration and significance of each mining stage in the life cycle. These features include the presence of a cocoon, window feeding, leaf cutting and construction of larval cases. Fly mines are readily distinguishable from moth mines, and occasional *Cladophora-*

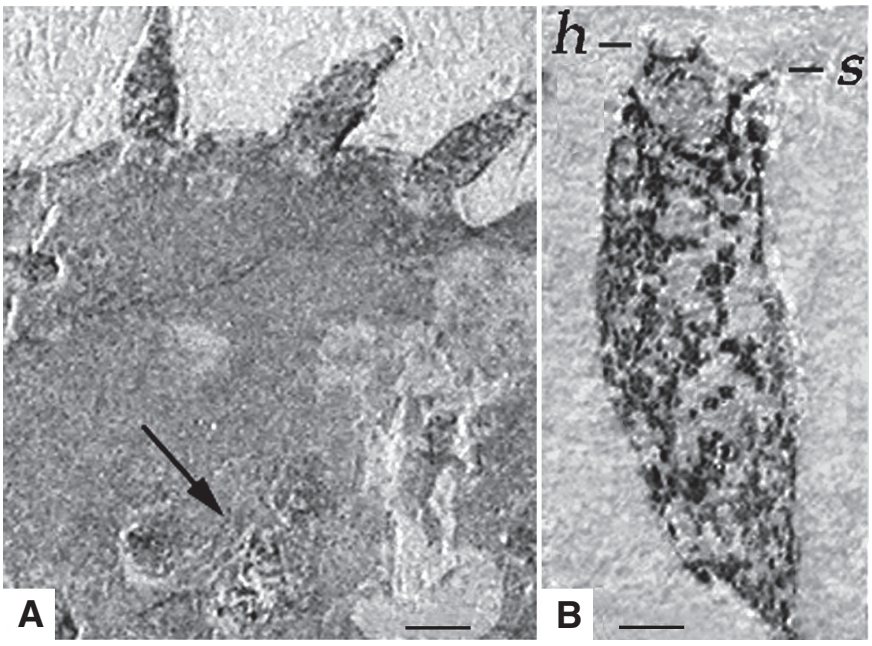

Fig. 6. Galls on Cretaceous leaves from the southern Negev: (A) fruit-like organoid galls on *Dewalquea gerofitica*, arrow on larva overgrown by developing gall, IG1-277; (B) abscised gall showing exuvial appendages (h, antennal horns; s, cephalic setae), IG1-110. Scale bars: (A) 1.2 mm, (B) 0.4 mm.

type mining (Hering 1951) is recognisable among the latter. Most of the mine types appear fairly modern, suggesting a fully developed mining habit. However, no extant analogues are found for certain types of mines on floating leaves, suggesting a possibility of extinct mining habits. Overlapping generations (Fig. 1C) indicate seasonality of mining activity, a potential source of climatological inference.

Although some leaf mines developing from the point of the petiole insertion caused deformities of the leaf blade (Fig. 2C), no intermediates between mining and galling were found. These two habits were as different in the Cretaceous as they are today. Galling habits were no less advanced than those of leaf mining, lending no support to the theory of their origin from one another (reviewed in Meyer 1987).

Galls are known since the Late Carboniferous (Van Amerom 1973; Labandeira & Phillips 2002), but advanced galling habits are commonly held to appear through gradual co-evolution of gall-inducing arthropods and angiosperms during the Tertiary (Ananthakrishnan 1984). Fossil evidence is inconsistent with this latter hypothesis. The mechanism of gall dehiscence by breaking loose from the leaf, as well as pupation in the gall rather than in the soil, are advanced developmental features (Mani 1964) that appeared in the mid-Cretaceous, at the critical stage of angiosperm–arthropod co-evolution. The role of galling as an organogenic factor in the evolution of early angiosperms is poorly understood, but some similarities of gall structure to the reproductive parts of the same host plant suggest that this role was significant.

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I acknowledge helpful comments and corrections by the reviewers of this paper, Drs C. Labandeira and J. Santiago-Blay (both Smithsonian Institution, USA). I am grateful to Dr Zeev Lewi and Mr S. Ashkenazi (Geological Survey of Israel) for their help in collecting material from the Gerofit locality.

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The entomofauna of the Lower Permian fossil insect beds of Kansas and Oklahoma, USA

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ABSTRACT

The Lower Permian Wellington Formation fossil beds of mid-continent North America are known best for the famous Elmo, Kansas locality. The Elmo site has produced tens of thousands of specimens from which more than 150 species of insects have been described. Equally productive and more widespread geographically, but less well-known, are the Midco, Oklahoma beds located some 270 km south of Elmo. The Midco beds have also yielded tens of thousands of specimens, but the material has been less well studied, and only half as many species have been identified from there. Renewed attention has been given in recent years to both the geology and palaeontology of the Wellington Formation. The history of these insect beds is recounted and the insect faunal composition is briefly reviewed. There are nearly 200 species in 106 genera, 53 families and 21 orders. Sizes (as measured by mean forewing length) range from 1.9 mm to 330 mm, with a mean of 22 mm and a median of 12 mm. Ten of 13 species with fore wings greater than 50 mm in length are Protodonata. Most species are known from one or a few specimens (abundance ranges from 1 to just under 400 specimens per species). Of ten species for which 50 or more specimens are known, eight are Grylloblattida (and six of these Grylloblattida: Lemmatophorina), indicating that these taxa were either quite abundant or were preferentially preserved, or both. When reviewing the holotype/neotype specimens used to describe the Wellington Formation species, we find that 62% consist of fore wings, while 9% are complete specimens. However, when considering all known specimens, 48% of the species are known only by their fore wings, while 13% are now represented by complete specimens, indicating the importance of continued collecting and review of Wellington Formation insect fossils.

KEY WORDS: Kansas, Oklahoma, Elmo, Midco, Lower Permian, Artinskian, Wellington Formation, fossil insects.

INTRODUCTION

The Lower Permian Elmo, Kansas, North American locality (Artinskian Age) is an important Palaeozoic fossil insect *Konservat-Lagerstätt*. Approximately 150 species of insects have been described from these beds, which were discovered by E.H. Sellards in the early 1900's. The Elmo locality insect-bearing strata are found within the Wellington Formation, which extends south from Elmo another 270 km to the vicinity of the city of Perry, Oklahoma, where the Midco fossil insect beds occur in a number of outcrops. The Midco locality, discovered by G.O. Raasch in the late 1930's, nearly a half century after Elmo, is less well studied; only half as many species are known from this locality. In the area between the Elmo and Midco localities, the Wellington Formation is covered by quaternary loess and alluvium and is exposed only in a few isolated locations. As a result, the only significant fossil insect beds are those at Elmo and Midco. Altogether approximately 200 species are known from the mid-continent Wellington deposits of Kansas and Oklahoma.

Little work has been done on the Wellington Formation insect fossils since the last paper on them by Frank Carpenter in 1979. However recent workers have begun to

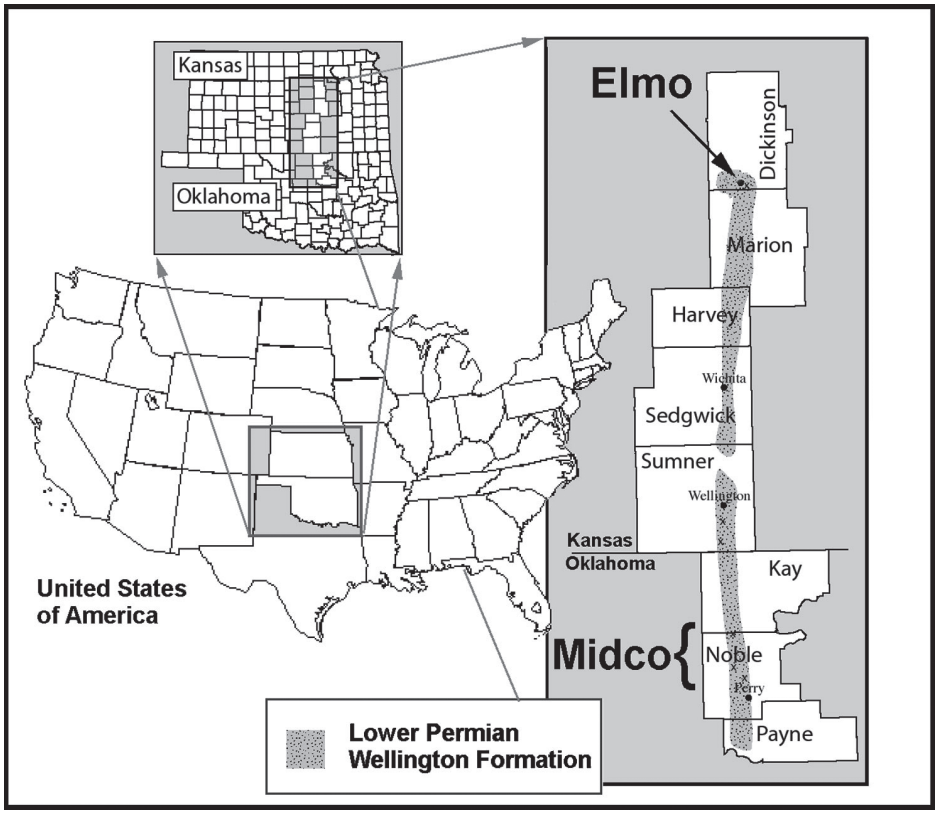

Fig. 1. Location and extent of the North American mid-continent Lower Permian Wellington Formation insect fossil deposits. The formation runs north to south some 270 km along eight counties, with major sites at the northern (Elmo, Kansas) and southern (Midco, Oklahoma) extremities.

reinvestigate both the geology and palaeontology of the Wellington. In this paper we briefly describe the location and the history of exploration of these insect beds, after which we review the Wellington Formation entomofaunal taxonomic diversity and size ranges as measured by forewing lengths, specimen abundance, and specimen quality.

LOCATION AND EXTENT

The Wellington Formation occurs close to the geographic centre of the contiguous United States in North America. It extends from north-central Kansas south through north-central Oklahoma (Fig. 1). The insect-bearing deposits lie along what was, in Permian times, a coastal plain or marginal marine environment (Dunbar & Tillyard 1924; Carpenter 1947; Raasch 1946). The Elmo beds are considered to have been fresh-water ponds or lakes while the Midco beds are thought to have been saline, possibly playa lakes (Carpenter 1947; Tasch 1964). Hall's (2004) recent reassessment of the Oklahoma Wellington Formation stratigraphy assigns the Midco beds to a marginal marine environment. The insects preserved as fossils are likely to have been allochthonous, and were either blown into the embayment by wind or washed into the embayment via streams (Hall 2004).

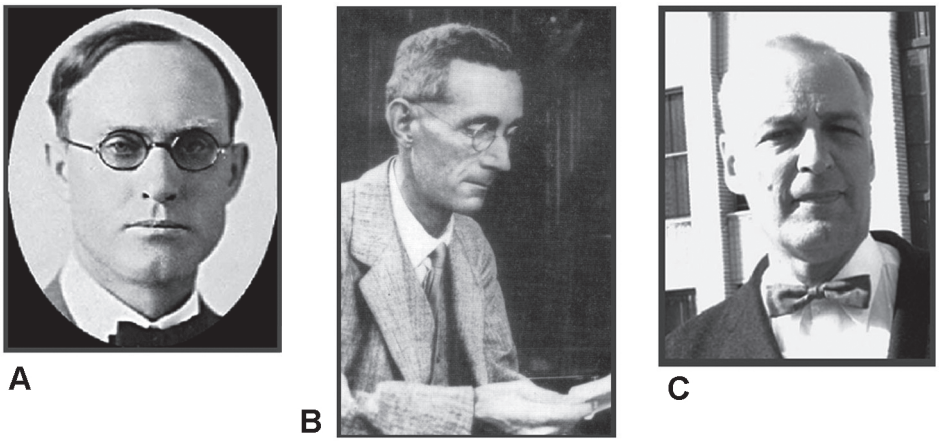

Fig. 2. (A) Elias H. Sellards (1875–1961) discovered the Elmo fossil beds (photo courtesy of the Texas Memorial Museum); (B) Robin J. Tillyard (1881–1937) studied Elmo fossils for a period of 16 years, carrying out his research in New Zealand and Australia. Eventually all the fossil specimens he worked with were returned to the Yale Peabody Museum (photo courtesy of the late Faith Tillyard Evans, Tillyard's daughter); (C) Frank M. Carpenter (1902–1994), of the Harvard Museum of Comparative Zoology and the dean of American palaeoentomologists, published definitive studies of the Elmo specimens over a period of some 60 years (photo courtesy of George Byers, University of Kansas).

HISTORICAL BACKGROUND

Elias H. Sellards (Fig. 2A) was studying Palaeozoic plant fossils under Samuel Williston at Kansas University in 1899 when he found two fossil insects among a collection of plant fossils from the Wellington Formation. He was interested enough to make trips to the locality, which was located near the small settlement of Elmo, Kansas (Fig. 3). He eventually collected some 2000 insect specimens. After completing a PhD at Yale University in 1903, he began a study of the Wellington Formation material, eventually describing many species, 27 of which are today recognized as valid. Sellards kept most of his specimens, but deposited a small representative collection in the Yale Peabody Museum.

In 1920, the distinguished entomologist Robin J. Tillyard (Fig. 2B), then residing in New Zealand and working at the Cawthron Institute in Nelson, was visiting Yale on a trip through the United States. He was excited to see a series of Sellards' fossil specimens in the Peabody Museum. His enthusiasm led Charles Schuchert and Carl Dunbar of Yale to obtain funding and embark on a collecting expedition to the Elmo beds. Another 2000 specimens were gathered. These were shipped to Tillyard in New Zealand, and he commenced a 16-year study of the material. Tillyard described 55 valid species of Elmo insects.

Frank M. Carpenter (Fig. 2C) began to work on Elmo fossil specimens in 1925. He published his last papers on them in the late 1970's. His prolific and definitive work on the Elmo fossils included revisions of taxa established by Sellards and Tillyard. Later, he also published on the Midco palaeopterous specimens (Carpenter 1947, 1979). Carpenter named a total of 96 valid species from Elmo and Midco.

E.B. Klots (1944) briefly discussed some protodonate and protozygopterous specimens from the Elmo beds, but did not describe any new species.

Fig. 3. The settlement of Elmo, Kansas, as it appeared in the early 1900's. The fossil beds, located a few miles southeast, were named after the town. (Photo courtesy of the Wichita State University Libraries Department of Special Collections.)

In the late 1930's, Gilbert O. Raasch (Fig. 4A) was working on a PhD in geology, studying the stratigraphy of the Wellington Formation in Oklahoma (Raasch 1946). He discovered a number of localities that were quite rich in fossil-insect material, and contacted Frank Carpenter. In 1940 the two men collected some 5000 specimens in ten weeks of field time. Subsequent collecting by Carpenter brought the total number of specimens from Midco in the Harvard Museum of Comparative Zoology collection to about 8000 (Carpenter 1979). Raasch eventually switched his interests to Cambrian trilobites of the Upper Mississippi Valley.

During the late 1950's and early 1960's, Paul Tasch (Fig. 4B), of Wichita State University, began working on the palaeolimnology of the Wellington Formation in Kansas and Oklahoma. He discovered insect fossils at a number of sites, and his associate, James Zimmerman, an entomologist from Wichita State University, eventually named eight species from the Oklahoma material (Tasch & Zimmerman 1962).

During the 1960's, Jarmila Kukalová-Peck studied a number of Wellington Formation taxa as part of her research on Palaeozoic insects. She reviewed the nymphal Ephemeroptera fossils collected by Carpenter from the Midco beds, determining them as the Wellington Formation genus *Protereisma*, but did not assign any specific names (Kukalová-Peck 1968). However, Demoulin, based solely on Kukalová-Peck's paper, assigned generic and specific names to her specimens in 1970. Hubbard and Kukalová-Peck (1980) and Carpenter (1979, 1992) eventually corrected Demoulin's work. The only valid Midco species named by Demoulin is *Protereisma americana* (Demoulin 1970).

A complete list of references to the Wellington Formation publications of the above researchers and a more detailed history of the Elmo locality have been published elsewhere (Beckemeyer 2000).

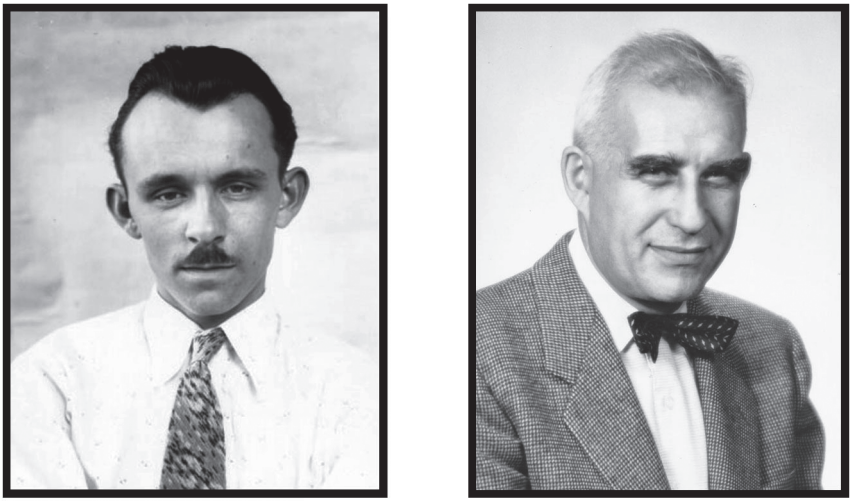

Fig. 4. (A) Gilbert O. Raasch (1903–1999) discovered the Midco fossil insect beds and documented the stratigraphy of the Oklahoma Wellington Formation in his PhD Thesis (Raasch 1946) (photo courtesy University of Wisconsin-Madison); (B) Paul Tasch of Wichita State University studied the palaeolimnology of the Wellington Formation in Kansas and Oklahoma and discovered additional Wellington Formation fossil insect localities in the late 1950's and early 1960's (photo courtesy of Wichita State University Department of Special Collections, Wichita, Kansas).

TABLE 1

Repositories of collections of Elmo and/or Midco Lower Permian Wellington Formation insect fossils.

Location	Collection Size/ Importance	Notes
Yale Peabody Museum	Major	Dunbar collection containing Tillyard's types
Harvard Museum of Comparative Zoology	Major	Carpenter's Elmo and Midco material: many thousands of specimens including types and large series
Texas Memorial Museum, University of Texas	Minor	Some of Sellards' type material
American Museum of Natural History	Minor	Klots protodonate and protozygoptera wings
University of Kansas Natural History Museum	Minor	Mostly Elmo material
Kansas State University Entomology Department	Minor	Some Elmo material including the Wenger-Holmes *Megatypus schucherti* counterpart
Oklahoma State University Entomology Department	Minor	Material from Midco
Wichita State University Geology Department	Minor	Some of Tasch's material, mostly from Midco, but with some Elmo material as well
Emporia State University	Minor	Mostly Midco material, comprised of the collections of the authors of this paper and including some type material

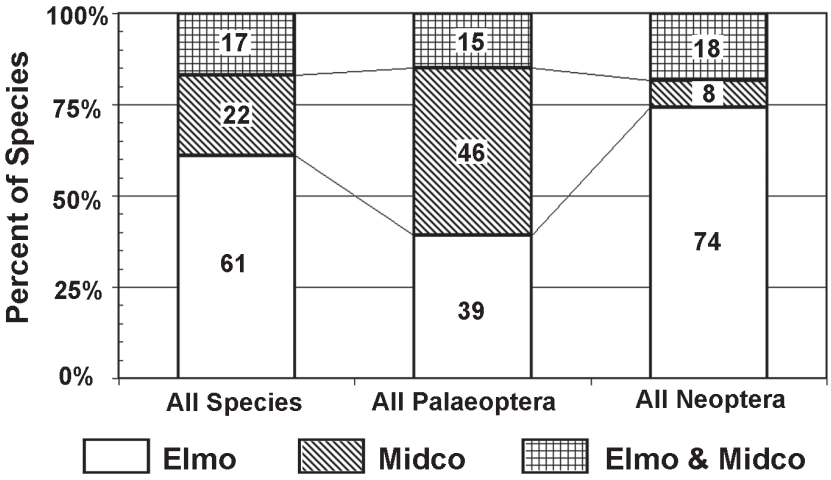

Fig. 5. Proportion of Wellington Formation entomofauna Neoptera and Palaeoptera subgroups unique to or shared between the Elmo and Midco localities, illustrating that the greater percentage of unique fauna at Elmo arises from the Neoptera. This reflects the fact that no review of the Neoptera from Midco has yet been published.

In recent times, beginning in the late 1990's, there has been renewed interest in the Wellington Formation entomofauana. Local workers, including Michael Engel of the University of Kansas and his students (Engel 1998; Lubkin & Engel 2005), and the authors (Beckemeyer 2000, 2004*a*, *b*, *c*; Beckemeyer & Byers 2001; Hall 2004) have started a fresh round of research. In addition, Béthoux *et al*. (2004) recently published a paper dealing with the order Caloneurodea from the Wellington Formation.

The Yale Peabody Museum and Harvard Museum of Comparative Zoology are the major repositories for the fossils, but there is a number of smaller collections (Table 1).

REVIEW OF THE ENTOMOFAUNA

Taxonomic diversity

A total of 194 valid insect species are currently known from the Wellington Formation; 118 (61%) are known only from Elmo, 43 (22%) are exclusive to Midco, and 33 (17%) are common to both localities. The lower number of species unique to Midco reflects the fact that Carpenter published only on the palaeopterous insects of Midco and not on the Neoptera (Fig. 5). Furthermore, there have been no reviews published or surveys conducted of Midco Neoptera. Since 1998, seven new Wellington Formation species have been described (Table 2) and seven species previously known from Elmo have been found to occur at Midco as well. Undoubtedly, many more species will be added upon a complete review of the neopterous material from Midco.

We compare the Elmo entomofauna distribution by major group (Holometabolous Neoptera, Paraneoptera, Polyneoptera, Palaeoptera, Apterygota) with the extant World insect fauna (figures for modern orders were taken from Grimaldi & Engel 2005) (Fig. 6). Insects with complete metamorphosis accounted for only about 7% of Elmo species, while today they are the most numerous of insects, accounting for approximately 83% of described species. Palaeoptera today account for less than 1% of the extant insect fauna while for Elmo, the group comprised nearly 27% of the species.

TABLE 2

New species added to the Wellington entomofauna since the publication of Carpenter's Treatise (1992).

Superorder	Order	Family	Genus	Species	Locality
Palaeoptera	Protodonata	Meganeuridae Handlirsch, 1906	*Megatypus* Tillyard, 1925	*parvus* Engel, 1998	Elmo
Neoptera	Caloneurodea	Uncertain Family	*Lipogramma* Béthoux *et al.*, 2004	*sinuosa* Béthoux *et al.*, 2004	Midco
Neoptera	Caloneurodea	Uncertain Family	*Gigagramma* Béthoux *et al.*, 2004	*carpenteri* Béthoux *et al.*, 2004	Midco
Neoptera	Grylloblattida: Protoperlina	Raaschiidae Beckemeyer, 2004	*Raaschia* Beckemeyer, 2004	*oklahomensis* Beckemeyer, 2004	Midco
Neoptera	Uncertain Order	Lophioneuridae Tillyard, 1921	*Cyphoneurodes* Bekker-Migdisova, 1953	*patriciae* Beckemeyer, 2004	Midco
Neoptera	Diaphanopterodea	Martynoviidae Tillyard, 1932	*Martynovia* Tillyard, 1932	*halli* Beckemeyer, 2004	Midco
Neoptera	Coleoptera	Uncertain Family	*Permocoleus* Lubkin & Engel, 2005	*wellingtonensis* Lubkin & Engel, 2005	Midco

Species diversity by major taxon (Order in most cases, Order: Suborder for the Grylloblattida) is shown for Elmo and Midco on Fig. 7. The ordinal system used is that of Carpenter (1992), with some modifications. Carpenter's "Protorthoptera" are placed in the Grylloblattida, Hypoperlida, and Blattinopseida, following Rasnitsyn and Quicke (2002). Classification of the Grylloblattida suborders follows Storozhenko (1998, 2002). Carpenter's Homoptera are grouped with the Hemiptera. The family Lophioneuridae is considered a stem group of Thysanoptera, after Kukalová-Peck (1991). The data are grouped into Apterygota, Pterygota: Palaeoptera and Pterygota: Neoptera sections, with the taxa arranged in each section in order of decreasing species diversity.

A nearly complete species list of Elmo insects may be found in Beckemeyer (2000). The Wellington entomofauna is quite diverse with 21 orders, 53 families and 106 genera represented.

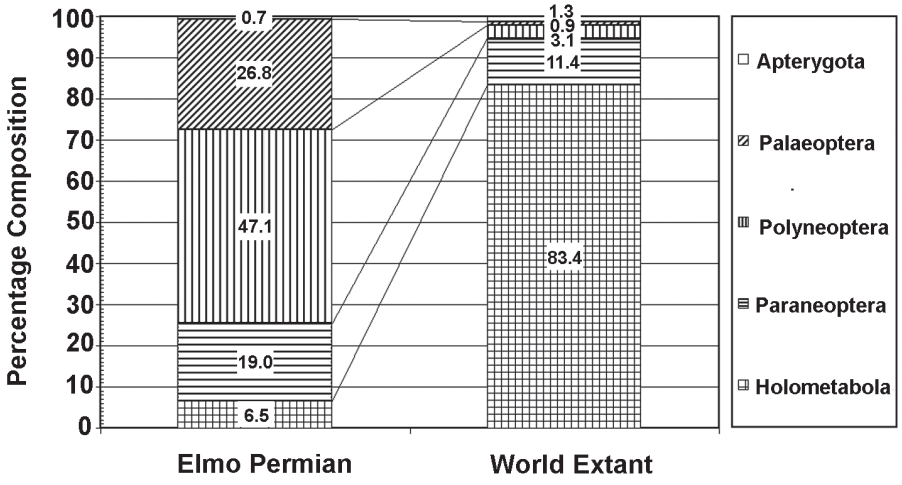

Fig. 6. Comparison of the distribution of the Elmo Permian and World extant entomofaunas by major groups: Apterygota, Palaeoptera, Polyneoptera, Paraneoptera, and Holometabola.

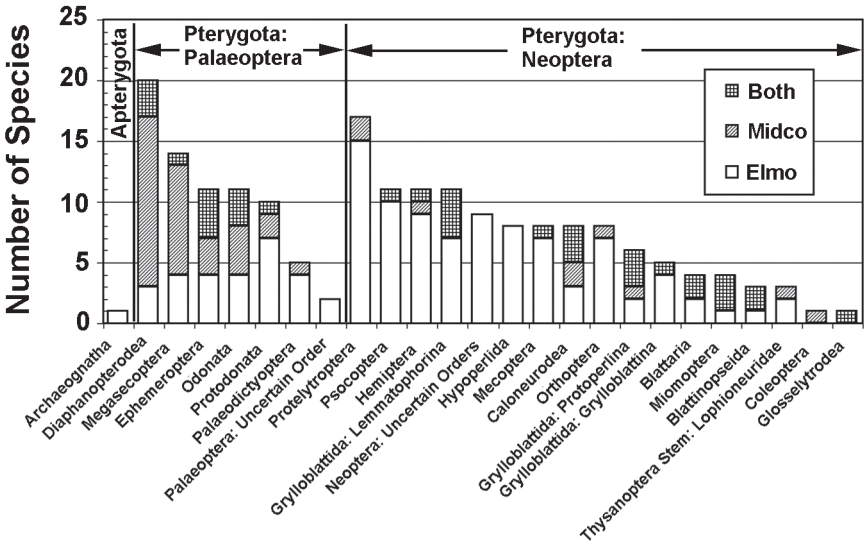

Fig. 7. Species diversity of the Wellington Formation entomofauna by Order (Suborder for the Grylloblattida). Orders are placed in three groups, Apterygota, Pterygota: Palaeoptera, and Pterygota: Neoptera, and are arranged in decreasing order of number of species. Bars show the number of species in each taxon unique to Elmo, unique to Midco and common to both. The nearly 200 species represent some 21 orders, 53 families and 106 genera.

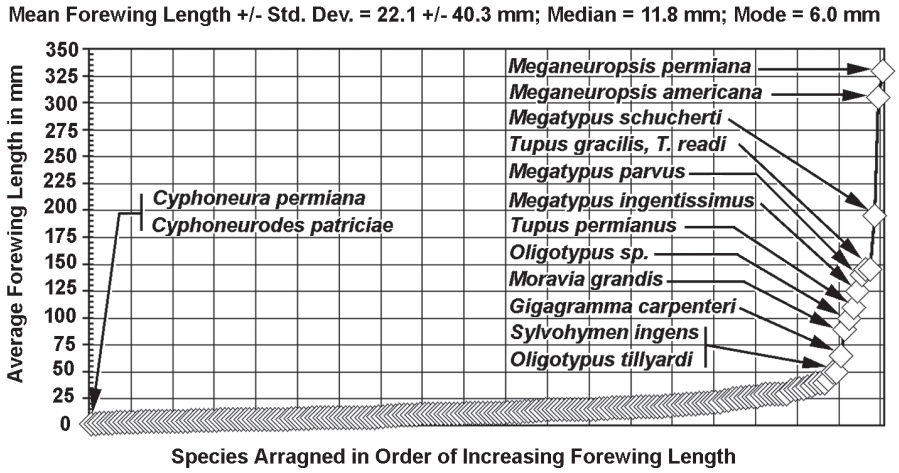

Fig. 8. Distribution of size in the Wellington Formation entomofauna. Size is based on average forewing length in mm, plotted from smallest species to largest species. The 13 largest (forewing length >100 mm) and 2 smallest (forewing length <2 mm) species are identified. The two smallest species are both in the family Lophioneuridae. Ten of the largest species belong to the order Protodonata; *M. grandis*, to Palaeodictyoptera; *G. carpenteri*, to Caloneurodea; and *S. ingens*, to Megasecoptera.

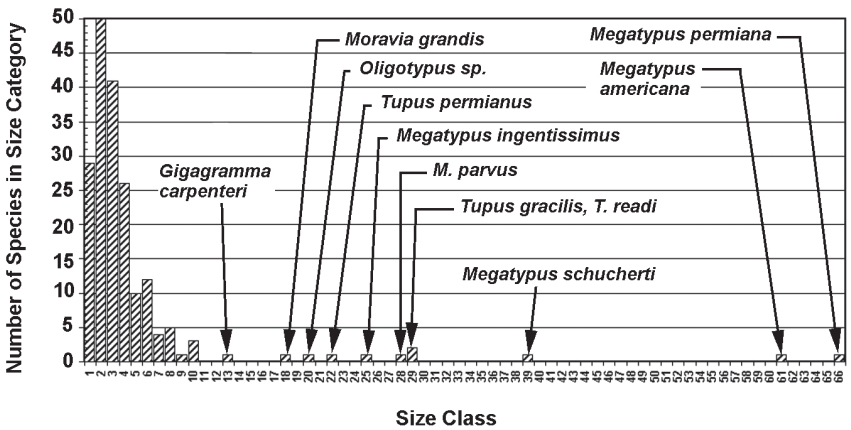

Fig. 9. Frequency distribution in 5-mm size classes of average forewing lengths for the Wellington Formation entomofauna.

Size diversity

The common view of Palaeozoic insects is that they were quite large, and, indeed, the largest insect known to have flown, the meganeurid *Meganeuropsis permiana* Carpenter, 1939, was described from the Elmo deposits. However, most of the insects of the Wellington formation were small, with fore wings less than 25 mm in length (Figs 8, 9). The mean length was 22 mm, the median 12 mm, and the mode 6 mm.

On Fig. 8, we have noted the species names of the insects with forewing lengths equal to or greater than 50 mm and those with forewing lengths less than or equal to 2 mm. Ten of the 13 insects with forewings of 50 mm or more were Protodonata. *Moravia grandis* is a palaeodictyopteran (Calvertiellidae), *Gigagramma carpenteri* is in the order Caloneurodea, and *Sylvohymen ingens* is in the order Megasecoptera. These are all extinct orders. The two species with the smallest forewings, 1.9 mm in length, are both in the Lophioneuridae, a family considered to be in a primitive stem group of the extant Thysanoptera.

Plotting forewing lengths in increasing size by taxon (order) (Fig. 10) gives an interesting observation that there is a fairly continuous gradation of size in most orders. This is even true of the Protodonata, a predatory order that contains most of the large species. However, in the three orders that contain a single large species (Palaeodictyoptera, Caloneurodea, and Megasecoptera), such species are the exception when compared to the majority of insects in these orders, which are much smaller and generally similar in size. It would be interesting to see analogous distributions for Carboniferous and Late Permian assemblages; one might anticipate a trend of decreasing size in these non-predatory groups from the Carboniferous, through the Lower Permian and into the Upper Permian, in response to selective predation by the large protodonates.

Specimen abundance

The number of adult specimens known per species in increasing order for the Elmo entomofauna is plotted in Fig. 11. The frequency distribution data for 10-specimen size classes are shown in Fig. 12. The mean is 21 specimens, but the median is 2 and the

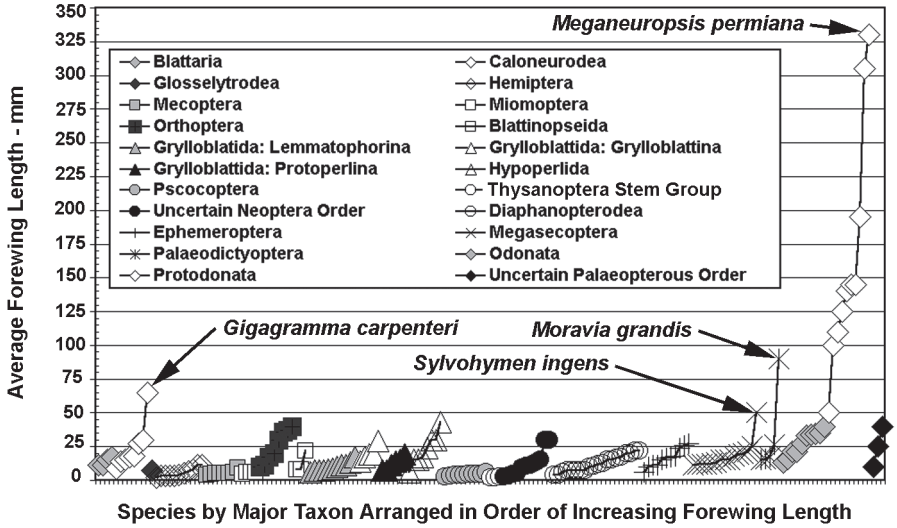

Fig. 10. Size distributions of the Wellington Formation entomofauna by major taxonomic groups. Size is based on average forewing length in mm.

mode 1. The high mean is due to half a dozen species for which large numbers of specimens have been found. Species for which more than a hundred specimens are known are identified in Figs 11 and 12. Of these six species, four (*Lemmatophora typa* Sellards, 1909, *Artinska clara* Sellards, 1909, *A. ovata* Sellards, 1909 and *Lisca minuta* Sellards, 1909) are Grylloblattida: Lemmatophorina: Lemmatophoridae. One species, *Probnis speciosa* Tillyard, 1939, belongs to Grylloblattida: Protoperlina: Probnidae,

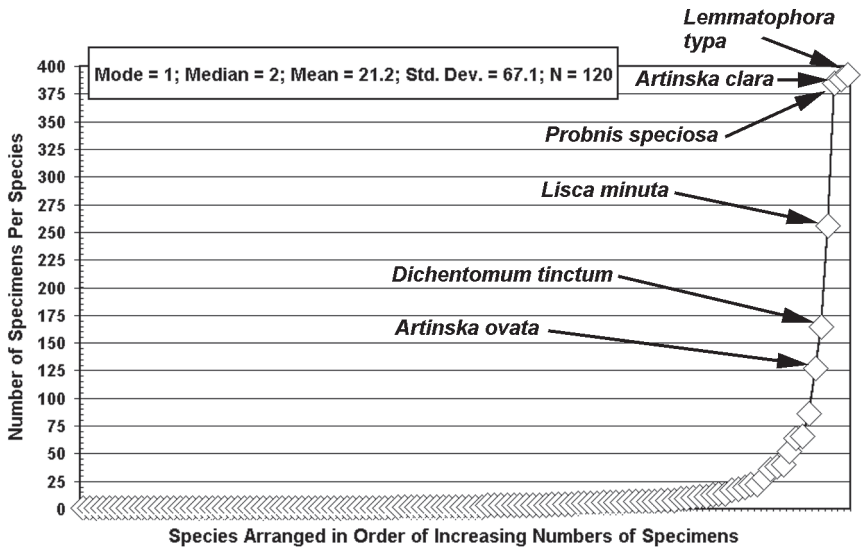

Fig. 11. Abundance of adult specimens of Elmo entomofauna. Values are plotted from species with fewest known specimens to species with the most known specimens. The species with the greatest numbers of specimens are identified. All labelled taxa are Grylloblattida except for *D. tinctum* (Psocoptera).

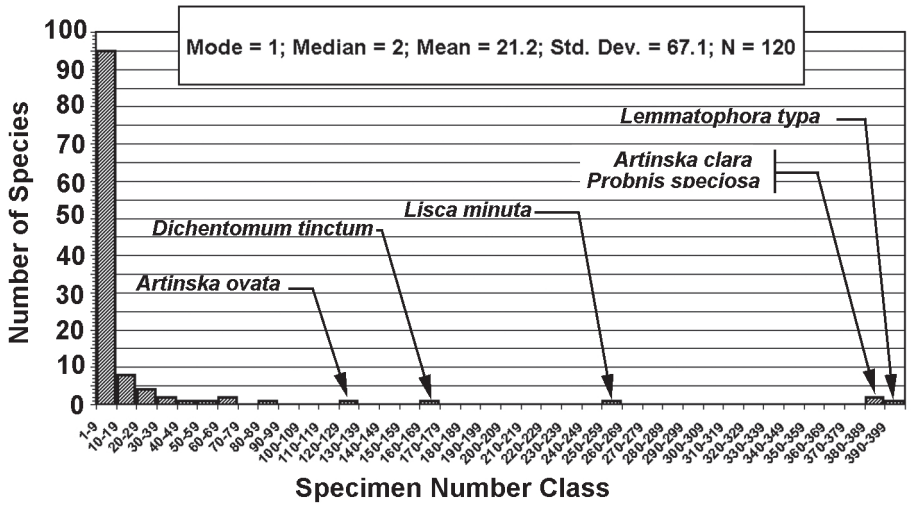

Fig. 12. Frequency distribution of adult-specimen abundance in 10-specimen size classes for the Elmo entomofauna.

and the last species, *Dichentomum tinctum* (Tillyard, 1926), is Psocoptera: Psocidiidae. Of the four species with more than 50 and less than 100 specimens, *Protereisma permianum* Sellards, 1907 (52 specimens) is Ephemeroptera: Protereismatidae, *Liomopterum ornatum* (Sellards, 1909) (86 specimens) is Grylloblattida: Grylloblattina: Liomopteridae, and the other two, *Lecorium elongatum* Sellards, 1909 and *Paraprisca fragilis* (Sellards, 1909), are lemmatophorids (66 and 64 specimens, respectively). Five of the six species with more than a hundred specimens and eight of the ten species with more than 50 specimens are Grylloblattida. Thus, the grylloblattids were either fairly abundant in the Elmo Permian, or they were preferentially preserved, or both.

Specimen abundance per species in increasing order of abundance by taxon is shown in Fig. 13. These taxa are plotted at the ordinal rank, except for the Grylloblattida, which are plotted at the Suborder rank. It is of interest to note that there is a relatively smooth distribution of abundance numbers for the Lemmatophorina, with nearly all the species in the family being well represented. For the other taxa which have species with a large number of specimens, most species in the relevant taxon have few specimens, and thus the well-represented species are exceptional. This can be seen in the Protoperlina, the Psocoptera, the Ephemeroptera, and several other groups. An interesting future study would be to determine if there are any obvious differences between the abundant and rarer species in these taxa that might account for their specimen numbers.

Nymphal vs. adult specimens

The great majority of the specimens from the Elmo locality are remains of adult insects. However, Carpenter (1935) reported 82 specimens of nymphs of which he determined to be at least two species of Lemmatophoridae, the family that is so well represented at Elmo by adult specimens. He based the separation of nymphal specimens on size, with nearly half being 9–10 mm in length and the other half 4.5–5.5 mm long. The larger specimens were considered by Carpenter (1992) most likely to be

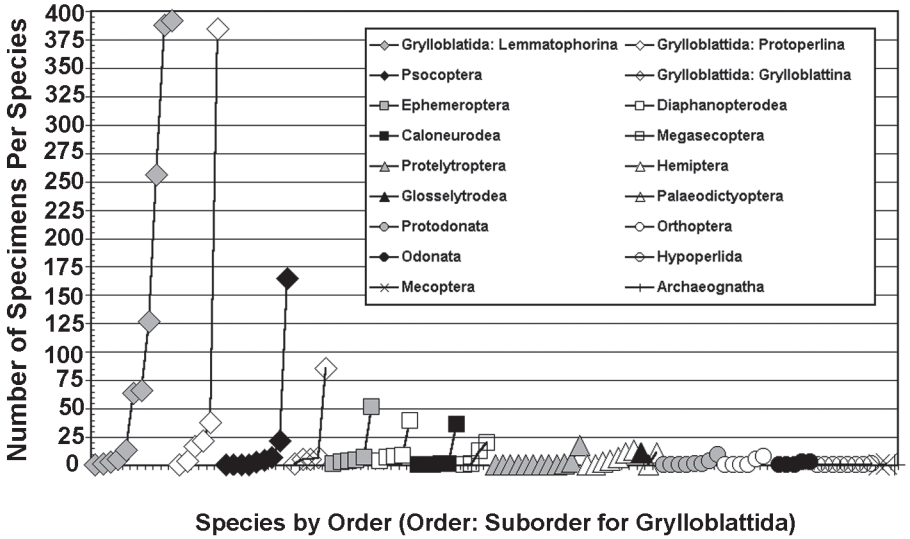

Fig. 13. Adult-specimen abundance distributions of the Elmo entomofauna by major taxonomic groups. Taxa are arranged in order of groups with greatest to lowest species abundance.

Lemmatophora typa, although definitive attribution could not be made. He considered the smaller nymphs most likely to be the species *Lisca minuta* or *Artinska ovata*. The nymphs possessed what appeared to be lateral gills on the first nine abdominal segments, and Carpenter (1935, 1992) stated that the nymphs were aquatic. However, later researchers consider these nymphs to be semi-aquatic (Storozhenko 2002) or even terrestrial (Aristov *et al.* 2006).

At Midco, Carpenter (1979) collected "several hundreds" of specimens of cast nymphal exuviae of Ephemeroptera of the family Protereismatidae. He noted that "Double that number were simply discarded in the field". This would likely make the nymphal protereismatids the most common specimens at Midco. More than 90% of Carpenter's specimens "consist of isolated wing pads from the nymphs and most of the remainder represent a single thoracic segment with the two wing pads attached." He also found several complete or nearly complete specimens. It should be noted that, over the past several years, the authors of this paper have found no similar fossils in collections from the Midco localities, so Carpenter's find may have represented a mass of exuviae washed in from a stream that emptied into the embayment.

Specimen quality

In the initial announcement of his discovery of the Elmo fossil locality, Elias Sellards (1903) noted: "A very large proportion of the wings are complete and their details of structure clear, even the minute hairs often being present." Another measure of quality is the wealth of information known about the morphology of the various insect species making up the entomofauna.

The distribution of species by the body part(s) by which they are known (fore wing, hind wing, wing, fore and hind wings, partially complete insects, and complete insects) is shown in Fig. 14. There are two sets of bars. The left bar in each pair represents the

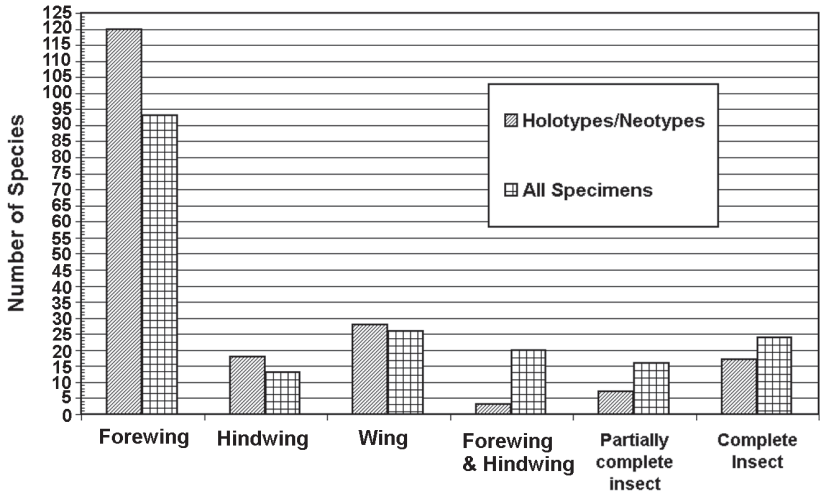

Fig. 14. Distribution of the Wellington Formation species by type of body part(s) for which species are known.

number of species with holotype or neotype specimens that comprise only the mentioned body part. The right bar represents the number of species presently known only by that body part. Thus, for the first pair of bars, representing forewing specimens, we see that 120 species have forewings as holotype or neotype specimens. When all known specimens are considered it becomes evident that hind wings, body parts, or even the complete insect are currently known for some of the taxa that were initially known only by their fore wings. Only 93 species are now known from their forewings alone.

The numbers of species known from various body parts on a percentage basis are compared in Fig. 15. These two charts illustrate the advantage of continued collections and studies of specimens after the species descriptions, and that much more knowledge can potentially be gained about the morphology of these insects.

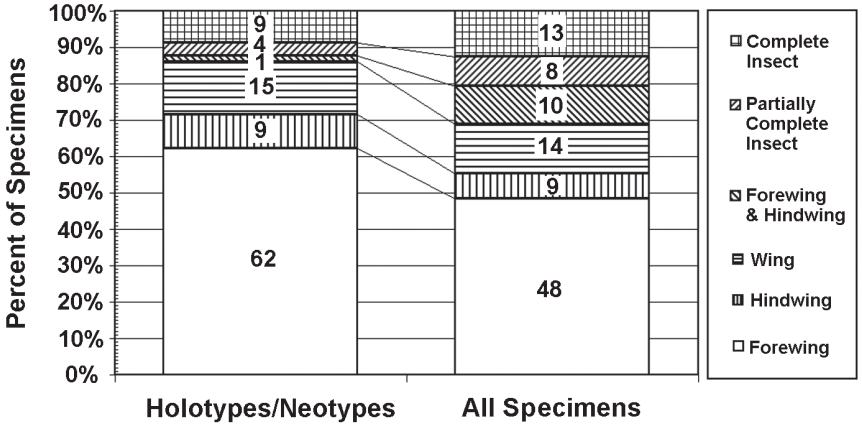

Fig. 15. Relative distribution of the Wellington Formation species by type of body part(s) by which species are known.

Fig. 16. Fore wing of *Stereopterum rotundum* Carpenter, 1950 (Grylloblattida: Lemmatophorina: Euryptilonidae), collected in March, 2004 from the Midco beds. An example of a species known only from its fore wing.

The authors recently collected a forewing from a locality in Noble County, Oklahoma (Fig. 16). It has been identified as *Stereopterum rotundum* Carpenter, 1950, a grylloblattid species that was described from Elmo. This specimen is the first record of the species from Midco. Just under half of all species from the Wellington Formation are known, as is this species, by fore wings only (Fig. 15).

Another fore wing collected from Noble County (Fig. 17A) represents one of two forewing specimens of *Chelopterum peregrinum* Carpenter, 1950 (Grylloblattida) known to the authors from the Midco, Oklahoma beds. This species also was described from Elmo material. However, additional Elmo specimens allowed Carpenter to reconstruct the entire insect. Based on Carpenter's reconstruction, an original drawing has been made by one of the authors (RJB) (Fig. 17B). As is typical, Carpenter's reconstruction of the insect shows it as if it were pinned in a display case, with its wings extended to illustrate the wing-venation patterns. Another drawing by RJB shows the species as it may have looked in life, with the wings folded over the abdomen (Fig. 17C). As noted in Fig. 15, complete insects are known only for 13% of the Wellington Formation species.

Another measure of the quality of the fossils from the Wellington Formation is what they may reveal about the insects that lived in the Permian. A case in point is the Elmo palaeodictyopteran *Dunbaria fasciipennis* Tillyard in Dunbar & Tillyard, 1924 (Spilapteridae). The species is known from only 10 specimens, but they are of excellent preservation, revealing information on wing colour patterns and morphology of the male and female external genitalia, as well as providing evidence of sexual dimorphism in the hindwing geometry (Kukalová-Peck 1971; Beckemeyer & Byers 2001).

CONCLUSIONS

The Kansas/Oklahoma Wellington Formation has been a major source of information on Lower Permian insect fauna for over 100 years, with nearly 200 species described to date. The Oklahoma beds are poorly known in comparison with the Kansas beds, but both sites meet the criteria for being *Konservat-Lagerstätten*: there is both an exceptional quality and quantity of fossil insect specimens found at these sites.

A number of species of Grylloblattida and one species of Psocoptera seem to be particularly abundant in the Wellington Formation. A study of the paleoecology of the

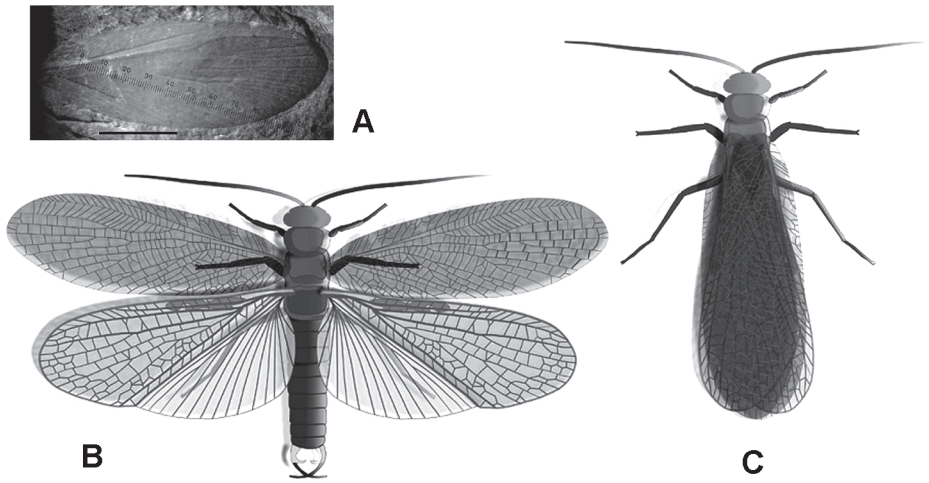

Fig. 17. *Chelopterum peregrinum* Carpenter, 1950 (Grylloblattida: Protoperlina: Chelopteridae), originally described from Elmo: (A) Photograph of fore wing of a specimen collected by the authors from the Midco beds, scale bar 5 mm; (B) Original drawing by Beckemeyer based on reconstruction by Carpenter (1992); (C) Original drawing by Beckemeyer of the insect as it might have appeared in life, with wings folded.

Wellington Permian might determine whether these insects were indeed more abundant or if they have been preferentially preserved, or both.

Large size seems to be a character of the Wellington Formation Protodonata, since 10 of 13 insects with fore wing lengths greater than 50 mm belong to this order. The orders Palaeodictyoptera, Megasecoptera and Caloneurodea each possessed one large species, with most of the Wellington Formation species in these orders being much smaller in size. It may prove beneficial to conduct a similar, complementary, analysis of the Carboniferous fauna, to explore whether there was a greater proportion of large species in these orders at an earlier time.

Much remains to be learned about the Wellington Formation entomofauna, both from unstudied material in current museum collections and from additional fossil material still to be discovered. It is especially important for the Midco Neoptera to be thoroughly reviewed, as there is currently no published, comprehensive survey of the Midco species.

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The geological setting and palaeoenvironmental and palaeoecological reconstructions of the Upper Permian insect beds at Belmont, New South Wales, Australia

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ABSTRACT

The entomofauna of the Tatarian insect beds within the Newcastle Coal Measures at Belmont, north of Sydney, was described many years ago. A new collection contains some undescribed species, particularly beetles; a new exposure of the fossiliferous deposits is now documented. The Newcastle Coal Measures consist of sandstones, conglomerates, shales, coal and tuffs, which were deposited in the Hunter Trough. The depositional environment consisted of a series of very shallow, stagnant freshwater pools along a gravel river channel system within a regional coal swamp. A volcanic event produced a volcanic ash dump, causing a "snapshot" kill of insects, validating possible interpretation of percentages of insect fossils in ecological modelling. The pool community included Conchostraca, *Permosyne* beetles and extremely rare insect larvae. A community on swamp banks adjacent to the water courses was comprised of *Glossopteris*-dominated flora and *Phyllotheca*, with an insect-dominated, first-level consumer community of phloem-feeding Hemiptera and possibly pollenivorous Mecoptera. A leaf-litter and bark-dwelling community included Protelytroptera, Psocoptera and archostematan Coleoptera. Neuroptera, extremely rare Trichoptera, and ancestors of the Orthoptera were also present in small numbers. Adult Neuroptera fossils suggest the presence of their predatory larvae and this group, along with the Odonata, are considered to have been the predatory components within this environment. No chelicerates, tetrapods or other potential top predators have been found in this, or proximal, facies. Disruptive colour patterns in some of the insects may indicate predator-prey relationships. Of interest also is the identification of a number of *Glossopteris* leaves with chewed margins. If these observations are correct, they would represent one of the earliest records of this kind of ichnofossil in Australia.

KEY WORDS: Insects, assemblage, *Glossopteris*, *Phyllotheca*, palaeoreconstructions, swamp, taphonomy, volcanic ash.

INTRODUCTION

This paper is an attempt to interpret the palaeoenvironment of the Belmont area during the Upper Permian based upon the evidence of sedimentary structures and facies relationships of the beds underlying and overlying the Belmont insect beds. The paper gives some preliminary findings of the proportions of the various insect orders and discusses ecological implications.

Geological setting

The Belmont insect bed is found within the Upper Newcastle Coal Measures of New South Wales (Fig. 1). The Belmont insect bed consists of a thin chert seam which is located within the Belmont Conglomerate Member within the upper part of the Croudace Bay Formation. The Belmont insect bed varies in thickness from approximately 20 cm to a reported 800 cm. At all sampled sites, over an area of outcrop of approximately 20 km^2, the bed varies in thickness from 20 to 32 cm, with the most common thickness being 30 cm. The Croudace Bay Formation consists of sandstones, conglomerates, coal and minor volcanic chert and shales (Diessel & Moelle 1988). The Belmont Conglomerate

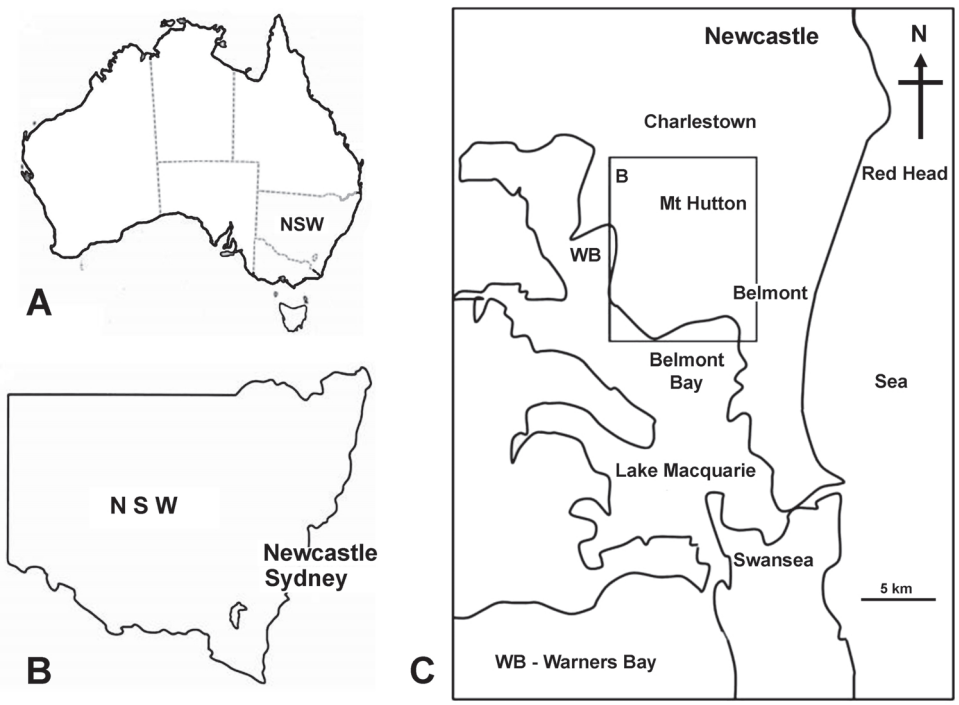

Fig. 1. (A) Outline map of Australia; (B) Outline map of New South Wales; (C) Map of Lake Macquarie area. The study area is enclosed in the rectangle.

filled an incised river valley and the stream, which deposited gravel within this valley, flowed in a south-southwest direction at approximately 210º (Herbert 1995). The gravel which filled the valley was sourced from the New England Fold Belt to the north-east (Little 1994), which was a highland region during the Permian. This river flowed into the Hunter Trough, which is part of the Sydney Basin, depositing gravel in the Belmont area, and sand further downstream, to the west, beyond Fennel Bay in the Lake Macquarie area (Engel 1966; Herbert 1995). The size of sediment grains decreased to the south-west (Brown *et al.* 1968). The Belmont Conglomerate is one of a number of lenticular fluvial bodies deposited during the Upper Permian in the Newcastle Coal Measures (Engel 1966). The volcano-clastic material deposited into the Newcastle Coal Measures during the Permian was sourced from volcanoes to the north or east (Wabrooke 1987). The Awaba Tuff and the Warner's Bay Tuff, above and below the Belmont Conglomerate respectively, thin out from north to south (Little *et al.* 1996). Marine sequences dominate the Early and Mid Permian of the Sydney Basin, but within the Upper Permian of the Newcastle Coal Measures the depositional palaeoenvironment grades upwards from beach-dominated coast and back-barrier swamps to braided plain, sheet-like alluvial fans and swamps. Coal-forming deposition proceeded throughout the Upper Permian of the Newcastle Coal Measures, which includes fourteen coal seams (Little *et al.* 1996; Wabrooke 1987) within a framework of transgression–regression cycles. Acritarchs have been found in strata immediately above the Croudace Bay Formation (Herbert 1995). The entire Newcastle Coalfield area was considered to be a high stand (Little *et*

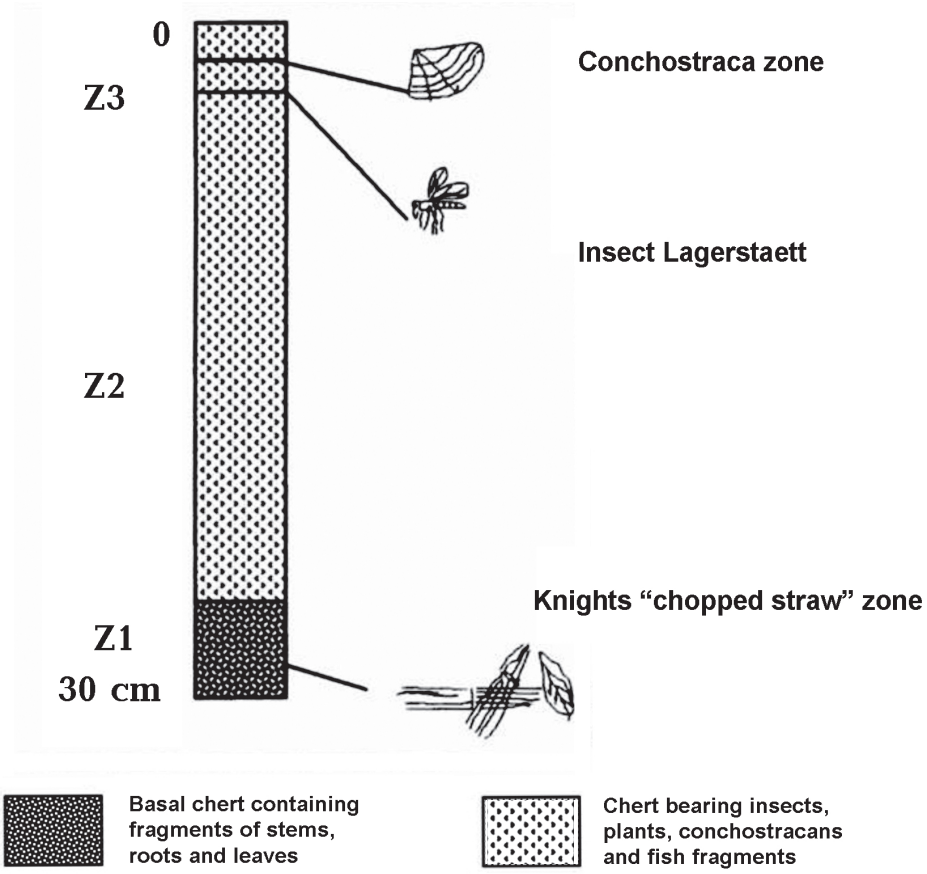

Fig. 2. Section of insect seam from Pincombe's Outcrop (site 206, see Fig. 3).

al. 1996) during the Upper Permian. Herbert (1995) considered the depositional conditions of the Belmont Conglomerate to represent a low stand, within Sequence H, which was probably deposited between 253 and 251 million years ago (P. Jones, pers. comm.).

Depositional Environment

Geology of the Belmont insect bed

The Belmont insect bed consists of a lithified volcanic ash (chert) (Tillyard 1926), represented by a fine groundmass of devitrified glass shards and fine phenocrysts, mainly consisting of feldspars, in addition to some opaque material. In thin section, the grains show linear alignment, and in sliced, insect seam blocks, fine horizontal bedding planes are visible. No cross-lamination has been observed. There is slight upward fining within the insect seam, more obvious in some specimens than others. The seam dips gently to the west and weathers to generally rhomboidal blocks. At most localities it has three distinct vertical zones. A section of insect bed from site 206 (Fig. 2) is typical of the sequence at all sites sampled along the Violet Town Ridge. At other sites there are

variations in the presence and thickness of a Conchostraca layer, in the zonation of the fossil insects and in the presence or absence of a basal layer known as the "chopped straw" zone (Knight 1950).

Zone 1. This is the lowest zone, and, where present, it consists of chert with a distinct appearance. It is grey, has a slightly coarser texture than the zones above it and has a fine groundmass with distinctly larger phenocrysts, which are generally linearly aligned. It also contains a large and instantly recognisable component of fossil phytobioclastic remains. This consists of highly fragmented stem sections of *Phyllotheca*, leaves of *Glossopteris* and sections of *Vertebraria* (roots of *Glossopteris*). These remains are chaotic and non-aligned. In general, Zone 1 is approximately 5 cm thick. Cut sections reveal no evidence of flow structures.

Zone 2. This zone has a slightly finer groundmass than that of Zone 1 and phenocrysts are much the same size as in the groundmass. The mineral composition of this zone appears to be the same as Zone 1. There is no fragmentary fossil plant component, except for occasional, isolated and very well-preserved *Glossopteris* leaves, becoming marginally more common towards the top of the zone. Zone 2 also contains very rare fossil insects and Conchostraca and is approximately 20 cm thick.

Zone 3. This is the uppermost zone. In the lowest layers it contains numerous well- to poorly-preserved *Glossopteris* leaves, seeds, fructifications, blackened carbonaceous leaf scraps and occasional *Phyllotheca* stems, usually found in unpredictable layers. Above it, there is a distinct insect-bearing layer, which also commonly contains well-preserved plant material, particularly *Glossopteris* leaves and less common fructifications, as well as Conchostraca, rare fish scales, fish scale clusters and a number of fish fins. The *Glossopteris* leaves are often complete, though sometimes crumpled. The layer varies from pale grey to yellow-white, and is often blotchy. Immediately above the insect layer, there is a Conchostraca (*Leaia*) layer, which contains abundant and easily-identifiable valves, both isolated and paired. In some rock slabs, the valves of Conchostraca are clustered. There are also occasional insect fossils embedded within this layer. Immediately above the Conchostraca layer, the chert is grey-white, blotchy and generally too weathered to reveal fossil content. Zone 3 is approximately 4 cm thick. At several sites, the non-ribbed conchostracan *Estheria* is found as well as *Leaia*. The Belmont insect bed outcrops in the Belmont area, north-west in the Kimbles Hill-Mount Hutton area, and to the west along the eastern shore of Lake Macquarie (Fig. 3).

Underlying Seam

The Belmont Conglomerate is widespread over the Belmont area and is exposed at various accessible sites including Brown's Outcrop, Burton Road, Croudace Quarry, 205, 206, and St Andrews Park (Fig. 3). This is a 41 m thick seam (Herbert 1995), with the thin insect bed being located near its middle part. Various facies ranging in thickness from 2 m to approximately 5 m occur between the top of the conglomerate underlying the insect bed and the base of the insect bed itself. These facies include coal, shale and fine sandstones, often in varied combinations at different sites. At most sites, weathered shale forms a layer directly beneath the insect seam. Fossil plant material within this shale is poorly preserved due to weathering. Coal has not been observed in direct contact with the base of the insect bed at any observed site. At one site (LCl, Fig. 3), sandstone is in direct contact with the insect bed.

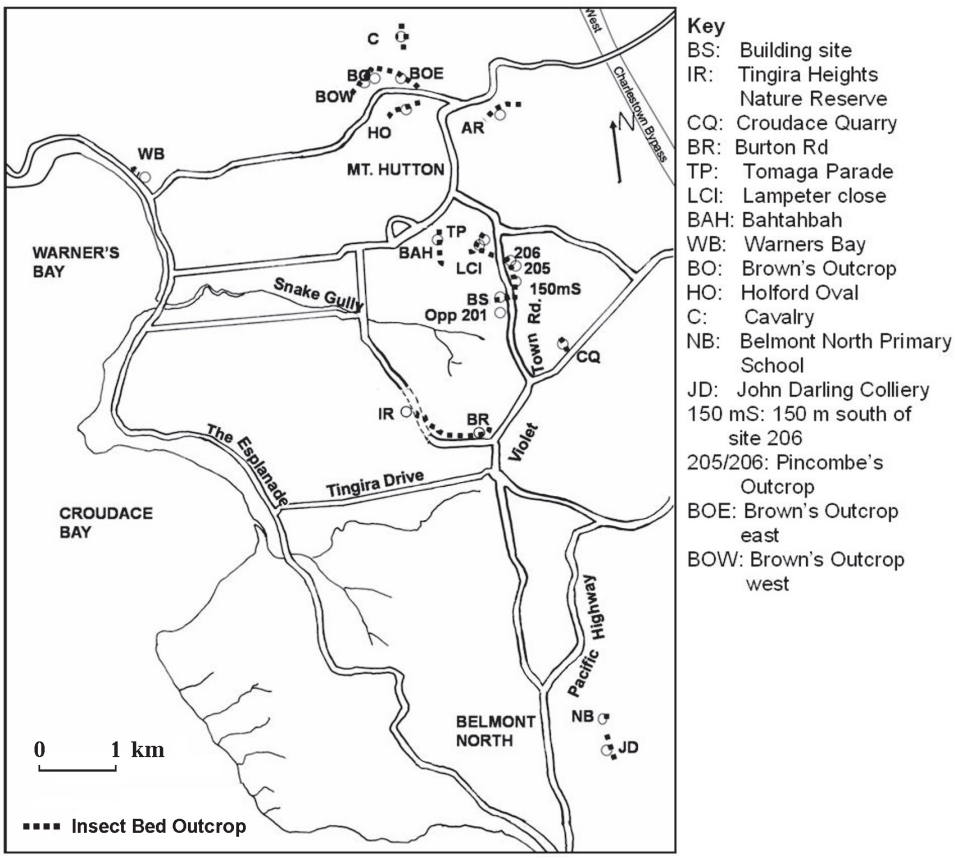

Fig. 3. Map of Belmont insect beds, showing new and old collection sites.

Overlying Seam

The rock in contact with the top of the insect bed is a fine sandstone and, where a section is exposed, this sandstone continues for at least 5 m, or there are alternate sandstone and conglomerate sequences (e.g., Brown's Outcrop), where the overlying seam is exposed vertically over approximately 30 m. A minor, discontinuous layer of shale exists within this overlying sequence at Brown's Outcrop.

MATERIAL

The author took great care to collect both parts and counterparts (when possible) for a new collection for the Australian Museum (approximately 800 specimens or 400 insects), and to collect and record as much data as possible for this study. The Richard Brown collection (Australian Museum) consists of approximately 80 specimens. The Australian Museum collection of fossil insects from Belmont consists of approximately 1500 specimens. Many counterparts are indicated, but it is unclear how many individual insects are actually in the collection. The original collectors donated specimens sporadically so that numbers of donated parts/counterparts may be quite different and

the relationship not recognised at registration. The Natural History Museum (London) collection consists of approximately 1000 specimens (A. Ross, pers. comm.), but the ratio of parts and counterparts is unknown at present.

TAPHONOMIC EXPERIMENT

A taphonomic experiment was conducted to observe the effect of a simulated volcanic ash shower on insect remains floating on an astatic water surface, in an attempt to find a mechanism to explain why some fossil insect wings are found below the Lagerstätten at the top of the Belmont insect bed. A one-litre jar was set up and partly filled with water. Insects were collected and sprinkled on the water surface. All the insects floated. A fine metal sieve was set up on the mouth of the jar. Gentle continuous dumping of a denatured cement powder into the container commenced in order to simulate an ash dump. Zones 2 and 3, of the Belmont insect bed, appear to have been formed by gentle, vertical ash accumulation. The majority of the experimental insects remained floating, despite this process of "ash" loading. Two insects submerged partially, and others actually sank to the sediment-water interface near the base of the container. This experiment may explain the mechanism by which insect remains are distributed. The mechanism appears to involve both increased ash load on floating insect parts, and the upward capillarity by water at the water-air interface on the "ash" load. Through saturation of pore spaces, the ash load becomes heavier, adhering to the insect remains which causes them to sink. If this is the case, then the majority of insects at Belmont insect beds have accumulated as a wing-float Lagerstätt, and the remainder have sunk and accumulated lower in the seam as a result of ash-loading.

PALAEOENVIRONMENTAL INTERPRETATION

Physical environmental evidence

The geometry and lithology of the Belmont Conglomerate is indicative of a major, upper-flow regime river channel, or channel system, grading into a lower-flow regime with a fining of facies further downstream (Brown *et al.* 1968). The Belmont area itself represents the braided channel part of this system, and the sandstone facies further south represent the delta-fan part of the system. Facies between the conglomerate and the base of the insect seam (coals, fine sandstones and shales) suggest an accumulation of overbank sediments adjacent to the river channel system, or possibly overbank sediments within the channel system itself. Overbank deposits of this type would be the result of overflow during flood times, in which the fines would accumulate on the bottoms of the ponds. Alternatively, these silty sediments could represent cessation of flow in the main channel system for an indeterminate time prior to the volcano-clastic deposition of the insect tuff layer. They may also indicate channel migration. Dunbar and Rogers (1957) found that thick sedimentary deposits are now forming at the foot of many of the mountain ranges in the United States, and that these alluvial fan deposits tend to have multiple channels with bedding approximately parallel to the fan surface, and with cross-stratification down fan in each channel and imbricated pebbles upfan. These characters are similar to those observed in the Belmont Conglomerate. Furthermore, Dunbar and Rogers (1957) found that such channel systems build up natural levees between them. It is likely that there were one or more channels, with

island and fringing levees within the channel system of the Belmont Conglomerate. Where abandoned channels connect with active channels, traps for silt and other fine-grained sediments can form, which create shoestring geometries corresponding with the original channel forms (Selley 1972). Deltaic floodplain has a significant proportion of silt-sized sediment (Folk 1968). Accumulations of this sediment therefore indicate low or no flow conditions as are commonly found in overbank ponds.

No autochthonous plant remains have been identified *in situ* in the decomposed shales directly underlying the insect seam, thus it is likely that trees were unable to establish in the overbank ponds because of water logging and poor aeration of roots. Evidence of Conchostraca (discussed below) also suggests that these overbank ponds were ephemeral. However, adjacent coal facies indicate co-existence with peat swamps which generated the coal deposits of the Newcastle Coal Measures and provide the abundance of fossil *Glossopteris* leaves, fructifications and some suspected autochthonous insects within the insect seam. The insect seam is thin, approximately 30 cm, apparently continuous and spatially widespread within the study area, notwithstanding general erosion of the area to ridges. This suggests that an isochronous "single dump" of volcanic ash resulted in the formation of the insect bed. Cut sections of blocks from the insect seam have no flow indicators such as cross lamination, or obvious sole marks along parting planes. This suggests that the ash was deposited in horizontal layers in non-flowing pools. The most likely model would be that the pools were either remnants of a drying main channel system, or overbank pools situated between the main channel system and the coal swamps. Zone 1 seems to grade abruptly into Zone 2, while Zone 2 seems to grade into Zone 3 without a clear break, giving the distinct appearance that the entire insect bed was deposited as a continuous process, which started with the sub-aerial dumping of shattered *Phyllotheca* stems from a directed volcanic blast, or from a lahar, followed by vertical deposition of ash and insect parts from the attendant ash cloud.

A possible sequence of events during formation of the Belmont insect beds is represented in Fig. 4. Stage 1 of the volcanic event is a directed blast (represented by the large horizontal arrow). This event shattered *Phyllotheca* thickets and carried debris, perhaps as a lahar, which settled into the bottom of overbank ponds in the D area of the diagram, to form layer C. In stage 2, volcanic dust from the attendant ash cloud (F) was steadily deposited onto the surface of the shallow overbank ponds. This filled up the ponds with volcanic mud E. During the process, conchostracans were forced to the surface, forming a layer, where they subsequently died. Insect remains were also deposited from the ash cloud onto the surface of the ponds D, where wings accumulated until they became incorporated into the wet volcanic mud. Other insect remains, and *Glossopteris* leaves were deposited from the swamp banks.

Fossil environmental evidence

The presence of fossil insects with aquatic immatures, such as *Nannochorista* (Mecoptera), and particularly of insects favouring cold, clear, pure, flowing water (Plecoptera) is strong evidence for a cold, lotic, depositional environment at Belmont (Tillyard 1935*b*). At the same time, there is contradictory fossil evidence of a Conchostraca bloom, in the form of highly abundant carapaces in the insect seam at almost all sampled sites. Modern Conchostraca generally live in ephemeral pools (Webb 1979; De Deckker, pers. comm.), which suggests low or absent water flow. It seems

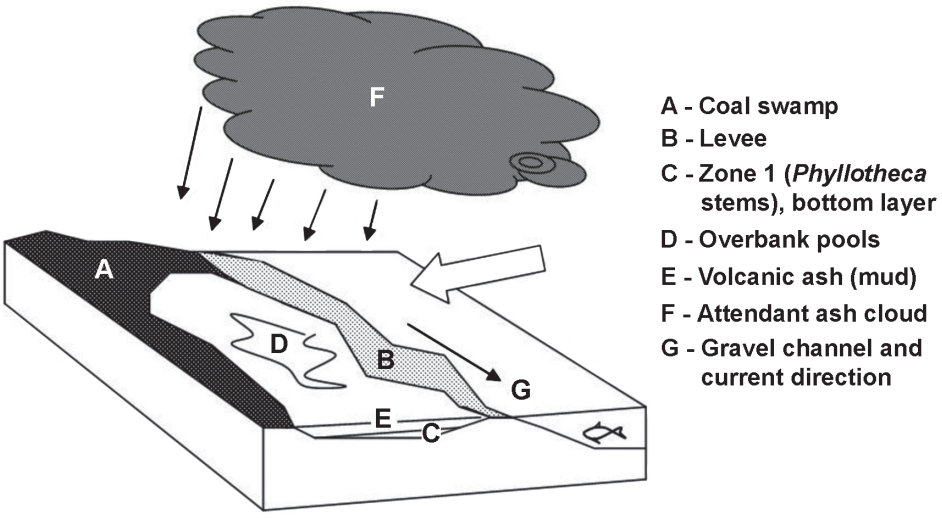

Fig. 4. A block model of the Belmont coal swamps and gravel channel system.

possible that before the tuff dump, a normally high-energy, gravel-depositing, perennial system stagnated for some time. Spillage into overbank pools ceased, and both the evaporation of, and seepage from, the pools triggered a Conchostraca bloom. If this is correct, then the Plecoptera larvae were either remnant entomofauna in the pools, or were washed into the pools by overbank spill from the main channel system prior to, or during the ash dump, as a result of storms which may have been associated with the volcanic event.

The abdomen of a Plecoptera nymph was found by Pincombe (Tillyard 1935*b*) and very recently, both a complete and partial Plecoptera nymph were found near Belmont by T. Annable (pers. comm.) in a fine sandstone within the Belmont Conglomerate at a horizon slightly above the Belmont insect bed. Occasional fish remains have also been found in the insect seam, including rare scales and even rarer fin parts. It is likely that fish might have been relocated from the main river channel into ephemeral pools during a flood or high flow prior to the ash event, became stranded and then died as the pools evaporated, stagnated and possibly became anoxic. Under these circumstances, the fish would have decomposed and disarticulated, becoming fossil components with the conchostracans and insects. At most sites, both conchostracans and insects are distinctly zoned, and fish remains, where recovered, are invariably found within the same upper part of the bed.

A possible mechanism explaining the distribution of Conchostraca in the insect bed can be suggested. After initial emplacement of disarticulated *Phyllotheca* stem sections, resulting from either a directed blast or a lahar mud wash, the volcanic ash fell as a continuous shower into shallow pools at least until the pools were filled. As the water became shallower, the Conchostraca were forced upwards until they became stranded in the evaporating pools. Conchostraca usually inhabit the bottom area of ponds (P. Jones, pers. comm.), but in this case, vast numbers were exposed to the effects of desiccation and perhaps heat and noxious volcanic gases, resulting in their death. The

retrieval of clumped fossil specimens may be indicative of this event. The fossil insects appear to be both allochthonous, presumably dumped out of attendant dust clouds from a volcano to the east, and autochthonous, from the leaf litter and foliage associated with adjacent swamp banks, and from the pools themselves.

Seasonal implications

Glossopteris leaves and fructifications are very abundant as the main plant fossils in the insect bed. *Glossopteris* leaf fossil accumulations suggest that this tree was deciduous (White 1998) and thus it is possible that the ash dump and insect seam formation occurred during autumn. However, it is also possible that the accumulation of leaves was caused by volcanic blasts, and therefore is not necessarily indicative of a season.

Allochthonous insect remains

Isolated wings constitute the bulk of insect remains (approximately 95% of insect fauna). It is probable that the majority of the wings were from insects which had suffered exposure to volcanic activity. If these insects were transported from between the volcanic source and the deposition site, then a winnowing effect probably caused a negative bias against body parts, and a positive bias in favour of wings. These wings were probably derived from insects further upstream and are assumed to be part of the same swamp/channel ecosystem (Fig. 5).

There are a number of insect remains of complete and partially complete specimens (approximately 5% of insect fauna). These are likely to have originated from two sources; from the swamp banks beside the ponds and from the ponds themselves. The majority of complete to semi-complete specimens are psyllids, a few psocids and beetles. The psyllids and psocids are likely to have inhabited the swamp banks, infesting the trees and shrubs; the Protelytroptera and grylloblattids probably inhabited the leaf litter, occupying the same niche as cockroaches today. Archostematan beetles probably inhabited rotting tree trunks, while *Permosyne* beetles inhabited the water surface and body of the pools. However, interestingly, there are other insects which might have been (at least partially) autochthonous, particularly the Mecoptera, which probably fed on the pollen provided by the abundant fruiting bodies and detritus. The less common Neuroptera would have preyed upon the abundant, sap-sucking Homoptera.

In terms of insect preservation, there appears to be an obvious bias toward smaller insects, i.e. the smaller the insect, the more likely it is to be preserved intact. Curiously, although there is a bias against large wings, the (often) large Protelytroptera wings are, almost without exception, completely well-preserved. There is little doubt that this is due to the toughening of the fore-wings in the form of elytra, but no other body parts have ever been found associated with these elytra. This is most surprising, since these insects probably lived in the leaf litter along the banks adjacent to the pools, and thus may not have been subjected to the full effect of volcanic activity experienced by the Mecoptera, Neuroptera and Odonata adults. The apterous immatures of Hemiptera are likely to have been present in significant numbers, inhabiting trees and shrubs; and yet few fossils of these immatures, relative to the abundance of preserved adult wings, have been found. A reason for this may be that wings of adults were more easily dumped into the pools from the banks than apterous immatures. Selected fossil insects from the Belmont insect beds are illustrated in Fig. 6.

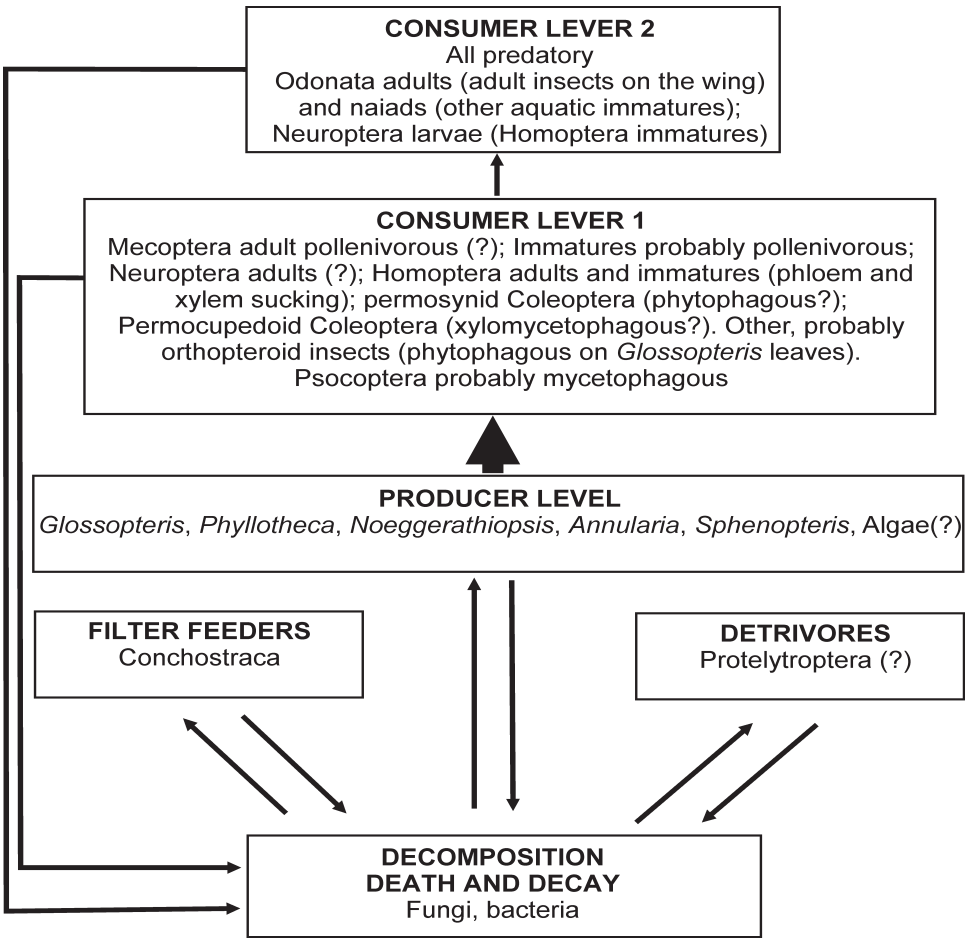

Fig. 5. An attempted reconstruction of the ecosystem of the Belmont coal swamp and overbank pools. The main component insect groups, conchostracans and plants preserved in the oryctocoenosis are illustrated here and assigned to definite, probable and possible feeding groups.

There is no evidence of *Glossopteris* tree trunks within the insect bed, apart from a few fossilised twigs, possibly from *Glossopteris* trees.

Palaeoflora

The preserved flora appears to be of low diversity, consisting primarily of the peltasperms *Glossopteris* and *Gangamopteris* and the sphenopsids *Phyllotheca* and *Annularia*. *Noeggerathiopsis* and *Sphenopteris* are also present. As mentioned above, the abundance of *Glossopteris* leaves might have been due to autumn fall. This means that *Glossopteris* may be overrepresented in the oryctocoenosis compared to *Phyllotheca*, which is most commonly represented by fossil specimens of stem sections rather than leaves. Their leaves are inconspicuous, generally highly fragmented, hard to quantify, and as a result may be underrepresented in the compositional analysis.

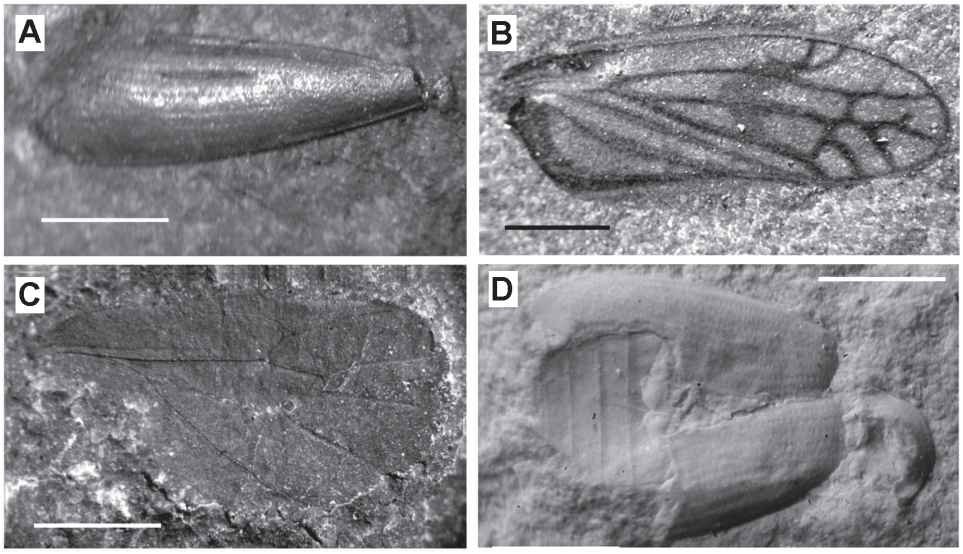

Fig. 6. Fossil insects: (A) *Permosyne pincombeae* (Coleoptera), holotype, Australian Museum AM F 19778 (original no. 14 T), note the indent, indicating the presence of a schiza, an adaptation to life in the water; (B) Wing belonging to an insect closely related to *Stenoviicia incerta* (Homoptera), specimen no. AM F 12948 (original no. B 325); (C) Wing of an undescribed protopsyllid (?) (Homoptera), specimen no. B 87; (D) *Permosyne mitchelli* (Coleoptera), specimen no. AM F 41273 (original number K129). Scale bars = 1 mm.

The peltasperms and sphenopsids form the primary producer basis for the Belmont ecosystem. Tillyard (1936) did not believe that sphenopsids were a food source for insects: "...nobody would accuse an insect with having anything to do with the Equisetales." However, there may have been a feeding association between flightless nymphs of an undescribed paraknightid (Hemiptera) and *Phyllotheca* in Permian strata in Siberia (Zherikhin 2002) and paraknightids are known from the Belmont region. Tillyard (1936) also identified what he considered to be a true choristid at Belmont and believed that this provided evidence of pollen eaters within the fossil insect fauna. The most likely food sources provided for insects by *Glossopteris* would have been phloem juices of the vascular tissue and the male fructifications, which would have provided pollen. There is also a possibility that these plants provided sugary rewards such as pollination drops, nectaries on vegetative tissues, and honeydew (see Labandeira 2002). Some insects may also have been folivorous, since chewed *Glossopteris* leaves have been found in the Belmont insect seam, and there is evidence of probable oviposition in the cambium tissue of *Phyllotheca* (Fig. 7B).

Disruptive colour patterns

A number of wings demonstrate chequered patterns while others show disruptive patterns. Such patterns have been observed in Mecoptera, Homoptera and Neuroptera. This may indicate predator or prey adaptations for camouflage within the dim and mottled light conditions of the coal swamps.

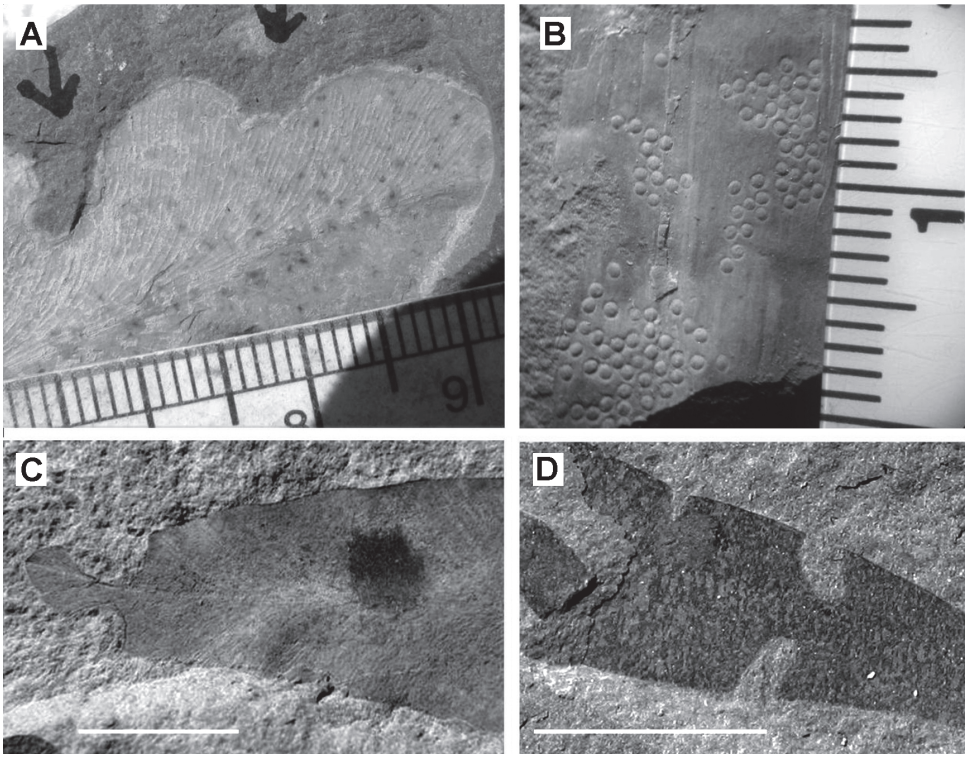

Fig. 7. Ichnofossils: (A) Chewed *Glossopteris* leaf margin, specimen BPl 3; (B) Probable insect eggs oviposited into a *Phyllotheca* stem, specimen AM F 122931; (C, D) Chewed *Glossopteris* leaf margins, specimens BPl 1 and BPl 2. Scale bars = 1 mm in Figs A, B and 1 cm in Figs C, D.

Plant–insect interactions

A number of chewed *Glossopteris* leaves and other presumed plant palaeopathological effects have been discovered very recently at Belmont during the collection of fossil insects. Specimens BPl 1 and BPl 2 (Figs 7C, 7D) are both discontinuous marginal chews and both are close to the apex of the pinnule. A number of other unnumbered specimens represent continuous chews along the pinnule margin (Fig. 7A). One specimen has been found in the Australian Museum collection on the "unidentified" Belmont fossil insect shelves, which consists of a small fragment of *Phyllotheca* stem, with embedded insect eggs.

PALAEOECOLOGY

Because elements within this ecosystem were most probably preserved as a result of a "snapshot" event, and the oryctocoenosis is similar to a thanatocoenosis, it seems reasonable to compare percentages of insect remains from different groups in terms of dietary guilds. This is further based upon the assumption that each single wing represents an individual insect (except, for example, where associated remains make it obvious that one individual is involved).

Percentage analysis was done based on the new collection (B collection). There is no obvious way of estimating biomasses involved at Belmont. However, ecological inter-

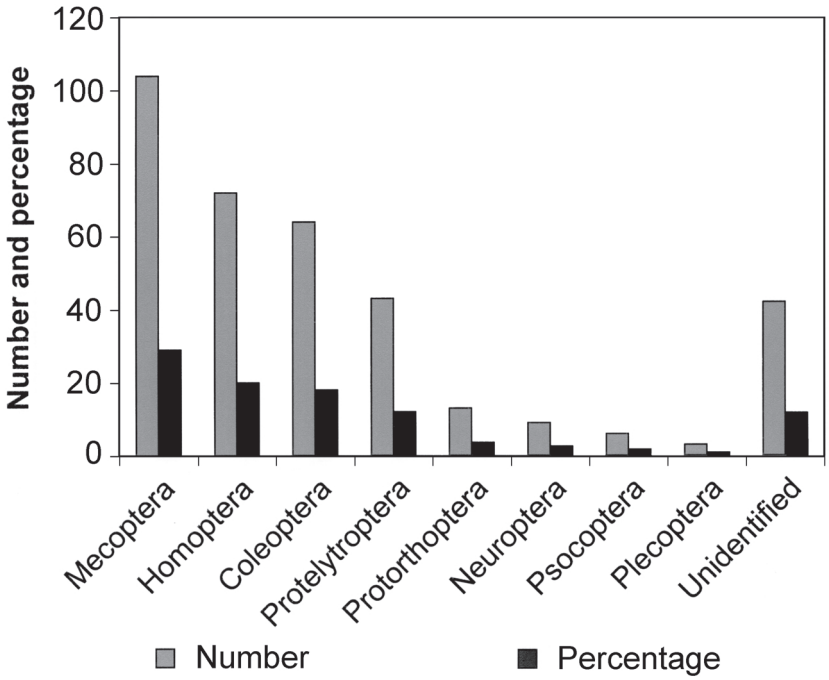

Fig. 8. Analysis of insect orders by number and percentage of individual insects (not total specimen numbers), Belmont insect beds, based upon new Beattie collection (2002–2004).

actions are suggested below, in order to illustrate feeding relationships. The most obvious insect predator–prey relationship in this ecosystem is that between neuropteran and homopteran immatures. No Neuroptera larvae were found but the remains of the adults of both orders indicate the presence of immatures within the biocoenosis and a few specimens of fossilised immature Homoptera exist in the Australian Museum collection. There are very few fossil remains of Odonata, but it would seem probable that these insects preyed upon flying insects such as the abundant Mecoptera. In this study, it is recognised that feeding behaviour in some of the fossil insect groups present at Belmont is unknown.

Four orders dominate the insect biocoenosis in the Belmont coal swamps and channel system, the Mecoptera, Homoptera, Coleoptera and Protelytroptera. Although subject to biases (as mentioned above), these data represent an approximation of the insect biocoenosis (Fig. 8).

The dominant Mecoptera family at Belmont was the Permochoristidae and the most abundant species was *Mesochorista australica*. Assuming the possibility that the direct ancestors of the Choristidae were the permochoristids, it is reasonable to consider that the two occupy a similar feeding niche. However, doubt has been shed on the relationships of extant Mecoptera to those of the Permian (D. Shcherbakov, pers. comm.). Tillyard (1922) believed the Permochoristidae to be pollenivorous, or an type of primary consumer, feeding on the abundant male reproductive bodies of *Glossopteris*, which are found as fossils in this seam, or dispersed pollen. Tillyard also believed that most of

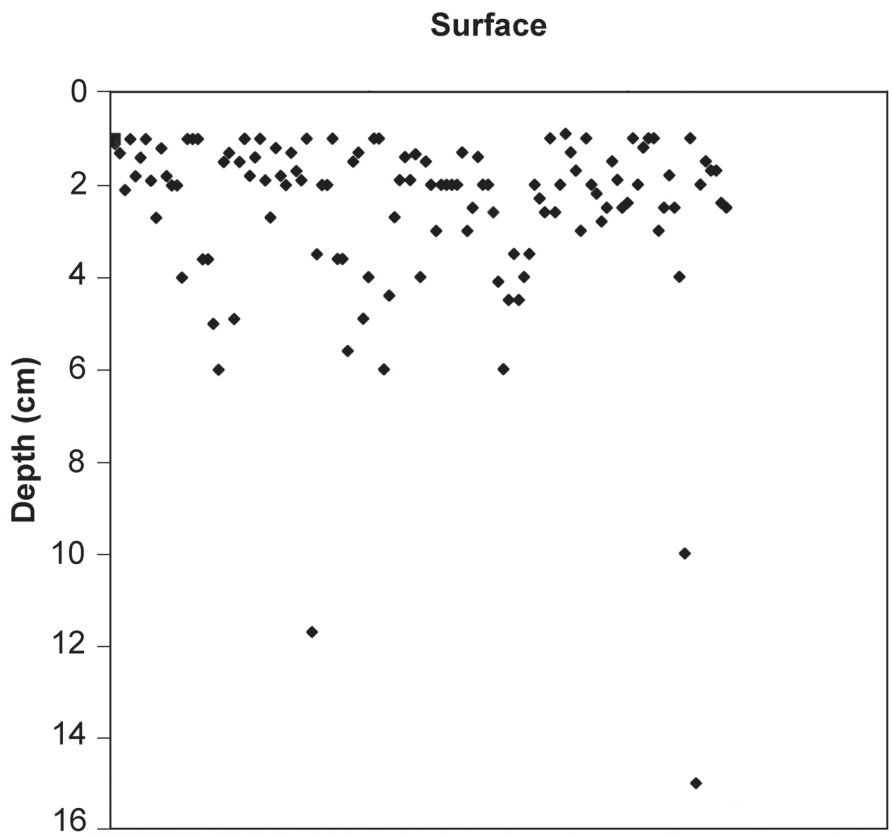

Fig. 9. Depth of fossil insects at site 205. Most wings are found in a Lagerstätt at a depth of 2 cm within the seam.

the other scorpionflies (and the Neuroptera) fed on the Hemiptera and Diptera, and considered the primitive scorpionflies to have possibly taken the place of the cockroaches (Tillyard 1922), which would make them detrivorous. The larvae of the *Nannochorista* (Mecoptera) possibly developed in pools and also fed on pollen banks in the leaf litter beneath the canopy (Strong *et al.* 1984).

The Homoptera are also significant primary consumers since Homoptera are regarded as phloem-feeders with highly specialised mouthparts for this purpose (Shcherbakov 2000), and some are xylem feeders. The plant community appears to have been largely bispecific, consisting primarily of *Glossopteris* and *Phyllotheca*, and thus it is likely that the Homoptera extracted the juices of these two plants.

In terms of the Coleoptera, high proportions of permosynids, *Permosyne belmontensis*, *P. mitchelli* and *P. affinus*, have been observed, with the most common being *P. belmontensis* and *P. mitchelli*. *Permosyne pincombeae* was also fairly common; the species has been transferred to the Rhomocoleidae (Ponomarenko 2003). *P. pincombeae* specimens have a distinct elytral groove not mentioned in Tillyard's original type description. This indicates a device for trapping an air bubble below the elytra for an aquatic mode of life (Ponomarenko 2002). Other beetles appear to belong to the families

Permocupedidae, Asiocoleidae, Taldycupidae and Schizocoleidae (Ponomarenko, pers. comm.), and the first three of these other families were bark beetles.

The Lophioneuridae probably fed on pollen and lived in the pollen sacs of host plants (Strong *et al.* 1984) while the Protelytroptera were the main scavengers of the leaf litter along the spongy swamp banks (assuming feeding habits were similar to that of their dermapterous descendants). Neuropteran immatures almost certainly preyed on homopteran immatures (Tillyard 1922). The Psocoptera probably grazed on fungi growing on tree and shrub trunks in this cold, damp environment. Modern grylloblattids, known as ice crawlers, feed on dying and immobilised insects. If there is an ancestral relationship, then there is a possibility that some of the fragmentary and poorly known grylloblattid fossils from Belmont had similar feeding habits, although they are the main suspects for folivory of *Glossopteris* in a Gondwanan flora of Brazil (Adami-Rodrigues *et al.* 2004).

CONCLUSIONS

The pre-eruptive environment during the Tatarian in the Belmont area consisted of the upper delta tract of a gravel channel system flowing through and within a regional coal swamp. A series of overbank ephemeral pools existed and probably periodically filled and then dried out over a number of years, building up layers of silty mud and sand of varying thicknesses. Prior to the volcanic event which resulted in the formation of the insect seam, a Conchostraca bloom had developed as the pools shallowed and started to dry out. A community of water beetles co-habited with the conchostracans. Fish trapped in these pools had died, possibly due to anoxia, and were in a state of advanced decomposition. Swamp banks beside the ponds were lined with *Phyllotheca*, *Glossopteris, Gangamopteris*, less common *Noeggerathiopsis* and rare *Sphenopteris* and *Annularia* plants. *Glossopteris* and *Gangamopteris* had lost the bulk of their leaves as a result of either seasonal change, or, more likely, by volcanic blast. Because Belmont was within Gondwanaland at a palaeolatitude of approximately 80º S, the ambient temperature was very low. A community of swamp insects existed based upon primary production by the swamp plants. A single volcanoclastic event occurred, depositing a blanket layer of tuff over the swamps and filling the shallow, ephemeral pools. The volcanic ash fall may have been uneven, resulting in thickness variation at particular sites. This event was energetic enough to deposit a layer of fragmented *Phyllotheca* stems and either the directed blast or a pyroclastic flow killed and disarticulated a large number of insects, which over time, fossilised within the ash-filled ponds. Homoptera and Mecoptera are the orders which are found to be most abundant at Belmont. It is almost certain that the Homoptera were primary consumers of plant phloem, and the Mecoptera (*Permochorista*) were primary consumers of pollen and also detrivores. The feeding niche of different groups of Coleoptera, including the rare bark beetles and probably the water beetles, was most likely that of xylomycetophagy and zoophagy, which would place them as secondary consumers. Of the identifiable higher-level consumers, the only definite examples are the Neuroptera and their immatures, which form a minor component of the fauna, in addition to the extremely rare Odonata. Other insect groups seem to have been involved in detrivorous and mycetophagous activities, associated with recycling, except for the rare Grylloblattida, which may have been, at least partly, folivorous. Fossil tetrapods have been found in strata much lower than at

Belmont in the Newcastle region (Warren 1997). Thus it is possible that these were the top predators within the ecosystem at Belmont.

In the final stages, river flow resumed along the channel system and the widespread deposition of sand, which encapsulated the tuff muds of the overbank ponds, allowed diagenetic processes to commence, resulting in lithification, and the preservation of the insect seam within the Belmont Conglomerate Member.

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The ecological role of immature phantom midges (Diptera: Chaoboridae) in the Eocene Lake Messel, Germany

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ABSTRACT

Autochthonous aquatic arthropods are only rarely found in the sediments of the Eocene Lake Messel. This has led to the assumption that certain abiotic conditions prevented a stable colonisation of aquatic groups. In recent years, the analysis of small fossil fish coprolites has shown that aquatic life was present in the former Lake Messel. A food web of different taxa of aquatic insect larvae and crustaceans was traced. Very abundant among the remains in the coprolites are larvae and pupae of phantom midges (Diptera: Chaoboridae). This article focuses on the survey of identified remains of immature chaoborids in the coprolites. In addition, it gives an outline of the major role that large populations of phantom midges can play in the pelagic ecosystem of a lake. Chaoborids are important both as prey for planktivorous fish and as predators of the smaller zooplankton. Via comparison with extant meromictic lakes, one can infer that the older phantom midge larvae displayed a vertical diurnal migration behaviour. They probably remained during the day within the anoxic water layers of the monimolimnion of the former Lake Messel to minimise the effect of predation by planktivorous fish. Lakes with large chaoborid populations are known to exist since the Jurassic.

KEY WORDS: Diptera, Chaoboridae, Tertiary, Eocene, Messel, palaeoecology, palaeolimnology, fish coprolites.

INTRODUCTION

The sediments of the fossil Lake Messel yield many exquisitely preserved fossils (e.g. Schaal & Ziegler 1992; Koenigswald & Storch 1998), among them thousands of insect remains. The insects are represented mostly by terrestrial groups (e.g. Lutz 1986, 1987, 1990; Tröster 1991, 1993*a*, 1994, 1999; Hörnschemeyer & Wedmann 1994; Wedmann & Hörnschemeyer 1994; Wappler 2003*a*; Wappler & Engel 2003; Wappler & Andersen 2004; Wedmann 2005). Analysis of the insect fossils provided interesting clues to the terrestrial environment of the former lake. Body fossils of autochthonous aquatic arthropods are rare (Lutz 1991; Tröster 1993*b*). Thus, the ecosystem of the lake itself was largely unknown for a long time.

In some other Palaeogene fossil sites aquatic insects also seem to be quite rare. For example, this appears to be the case in the volcanic basins of Eckfeld (Eifel, Germany) and Enspel (Westerwald, Germany), where the insect oryctocoenoses were analysed by Wappler (2003*b*) and Wedmann (2000). The size and shape of the sedimentary basin had a very important effect on the composition of the taphocoenosis.

The geographic position of Lake Messel is illustrated in Fig. 1. Today, the locality is situated about 8 km north-east of Darmstadt in Germany. Until some ten years ago the Messel pit was destined to become a rubbish tip. Since 1995, it is on the World Heritage List, mainly because of its wealth of fossil mammals. The fossils are embedded in the so-called “oil shale” sediments. This is a siltstone that contains kerogen mainly originating from algae. The sediments were formed under anaerobic conditions in a deep meromictic lake (Goth 1988, 1990). The lake was permanently stratified, where a

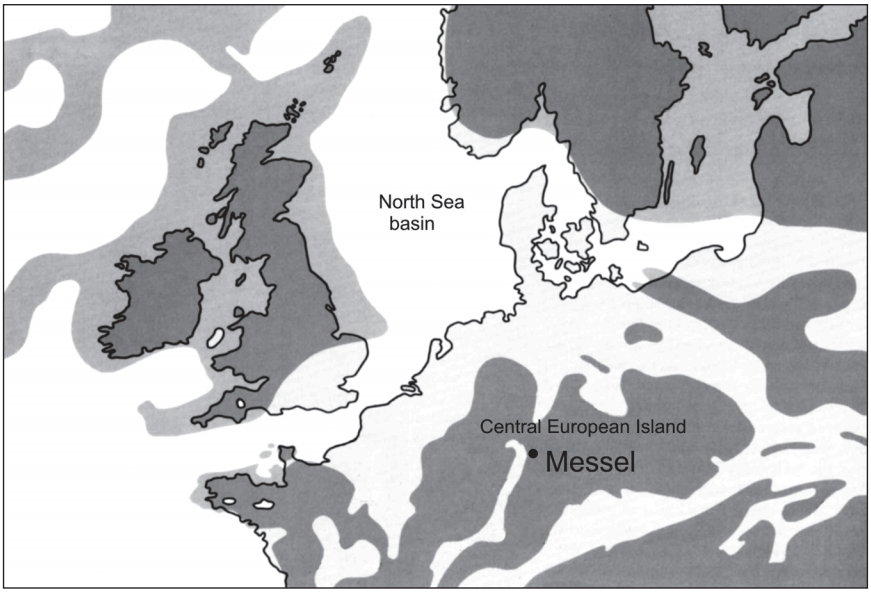

Fig. 1. The geographic position of Lake Messel during the Eocene. White indicates sea, grey indicates land during the Eocene. The outlines of present-day northern Europe are superimposed. Modified after Franzen (1992).

chemocline separated the upper part of the water body, also called mixolimnion, from the lower part, the monimolimnion. Life was possible only in the mixolimnion. The monimolimnion was anoxic and also had a higher salinity.

A core drilled in 2001 revealed that Lake Messel was a maar lake with an initial diameter of about 1.5 km (Harms 2002). Maar lakes have their origin in a volcanic steam explosion. According to recent research, the sediments of Messel were deposited about 47 million years ago (Mertz *et al.* 2004).

Until some years ago, the rarity of autochthonous water-living arthropods in the sediments of Lake Messel seemed to support the assumption that special abiotic conditions prevented colonisation of the lake by aquatic groups (Lutz 1987, 1990; Rietschel 1988). Autochthonous insects and water fleas were first reported by Lutz (1991). Richter and Krebs (1999) identified nymphs of mayflies (Ephemeroptera) from the sediments and interpreted their presence as indicating that Lake Messel had not been as hostile as supposed previously. As further studies showed, the scarcity of body fossils of aquatic arthropods did not indicate an absence of aquatic life in the lake. Through the analysis of small fish coprolites, that can be found quite frequently in the sediments, it was possible to discover a food web in the pelagic zone of Lake Messel (Richter & Baszio 2001*a*, 2002). Examination of gut contents showed that the main producer of the so-called 'type A' coprolites were small fish of the species *Thaumaturus intermedius* Weitzel, 1933 or juvenile stages of other fish species occurring in the lake (Richter & Baszio 2001*b*). Specimens of *T. intermedius* reached a maximum length of 90 mm in Lake Messel, however most fossils recovered are 30 to 70 mm long (Micklich 2002). Fossils of this fish species are found quite often in the sediments. Type A coprolites contain a variety of chitinous remains of different aquatic invertebrates. Identified

structures belong to the larvae and pupae of phantom midges (Chaoboridae), larvae of mosquitoes (Culicidae) and chironomid midges (Chironomidae), mayfly nymphs (Ephemeroptera) and small crustaceans (Cladocera and juvenile Conchostraca) (Richter & Baszio 2001*a*, 2002; Richter & Wedmann 2005). Many other fragments remain to be identified. An absence of small fish coprolites from basal sediments of the core of the 2001 drilling project indicates that apparently no significant planktivorous fish population existed during the initial stages of Lake Messel (Richter & Wedmann 2005).

The aim of this paper is to discuss the ecological significance of chaoborid remains found in the type A coprolites.

MATERIAL AND METHODS

About 500 small fish coprolites were studied. Some of the fish coprolites come from sediments with a stratigraphic range of a few meters around the key horizon alpha, where excavation is currently taking place. The remaining coprolites originate from the drilling core of the 2001 Messel pit research drilling project.

The coprolites of type A are very flat, not mineralised and flexible when humid. They are either round with a diameter of up to 12 mm or elongated and ribbon-shaped, up to 25 mm long (Fig. 2). Freshly collected coprolites can be separated from the sediment matrix quite easily.

The coprolites were dehydrated and embedded in Canada balsam (Richter & Baszio 2001*a*). When investigated with transmitted-light microscopy many interesting structures are visible (Fig. 3; Richter & Baszio 2001*a*).

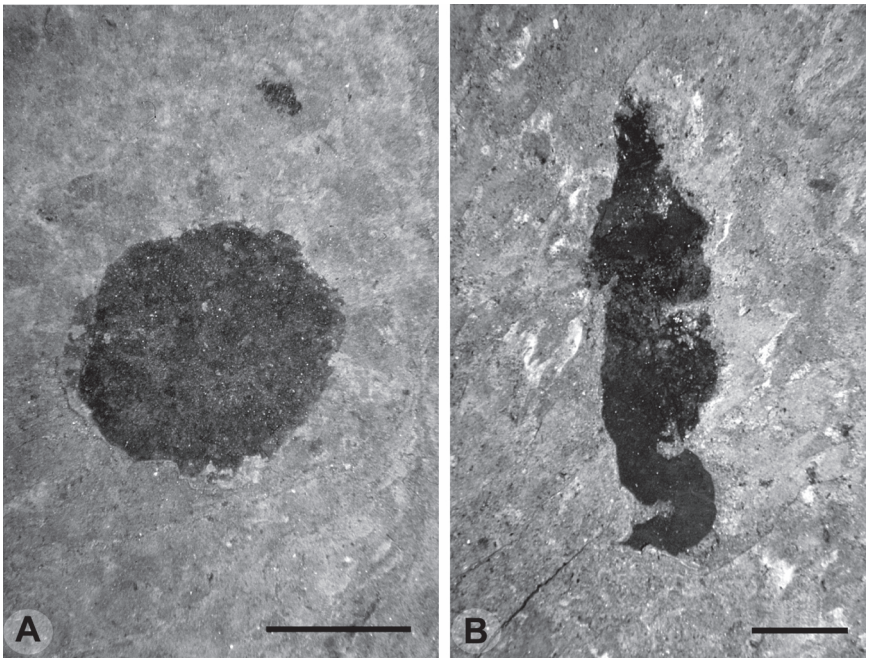

Fig. 2. Coprolites of so-called type A which exclusively contain remains from aquatic living invertebrates: (A) round coprolite; (B) elongated coprolite. Incident light microscopy. Scale bars 5 mm.

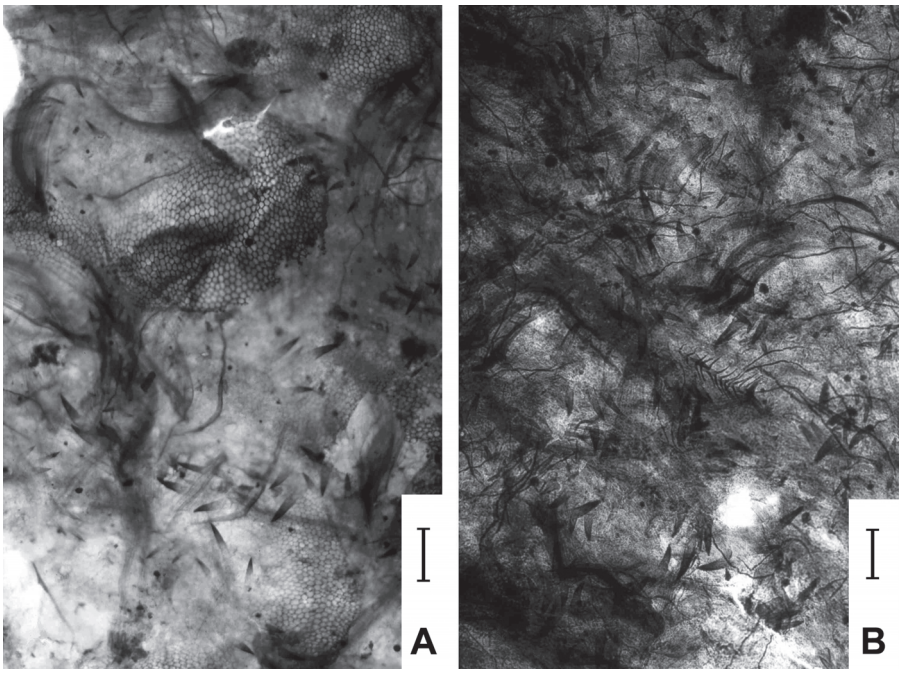

Fig. 3. Isolated type A coprolites viewed using transmitted-light microscopy. Scale bars 100 µm.

The number of identifiable remains in coprolites was roughly estimated. It must be noted that many remains that are present in the coprolites are not yet identified, so the results of this analysis are preliminary.

RESULTS AND DISCUSSION

Remains of immature phantom midges are common in the coprolites from Messel. More than 90% of the coprolites studied contain them.

The mandibles of *Chaoborus* larvae are particularly common (Richter & Baszio 2001*a*). They consist of a characteristic set of four dark-coloured spines (Fig. 4). The mandibles are often found in pairs (Fig. 4A). In some coprolites, mandibles of different sizes are present (Fig. 5). This indicates that different larval instars of chaoborid midges coexisted in the ancient lake (see discussion of chaoborid life cycle below). Figure 6 shows characteristic groups of cirri, which constitute a part of phantom-midge mandible bases (Richter & Baszio 2001*a*). Structures difficult to find are pairs of small, transparent caudal hooks (Fig. 7A), which are located on the last abdominal segment of *Chaoborus* larvae. Remains with a fan-like row of setae (Fig. 7B) can also be found (Richter & Baszio 2002). Unambiguous assignment of this structure to phantom midge larvae is impossible because such anal fans are known in larvae of three nematoceran families, i.e. Corethrellidae, Culicidae, and Chaoboridae (Wood & Borkent 1989). Another rare find is a paddle-like structure in a coprolite (Fig. 7C). Similar structures can be found at the apex of the abdomen of pupae of chaoborid midges (see Fig. 9B). This kind of membranous paddle with a supporting midrib and additional ribs on each side is characteristic of *Chaoborus* pupae (Sæther 1997).

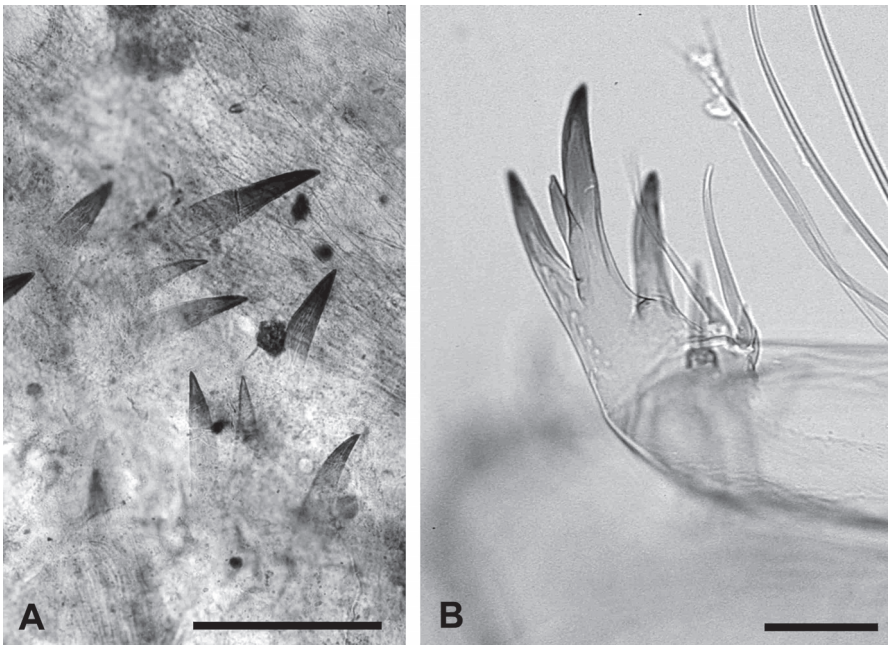

Fig. 4. Parts of mandibles of phantom midge larvae (Chaoboridae): (A) fossil structure in a coprolite; (B) part of a mandible from extant *Chaoborus* sp. Transmitted-light microscopy. Scale bars 100 µm.

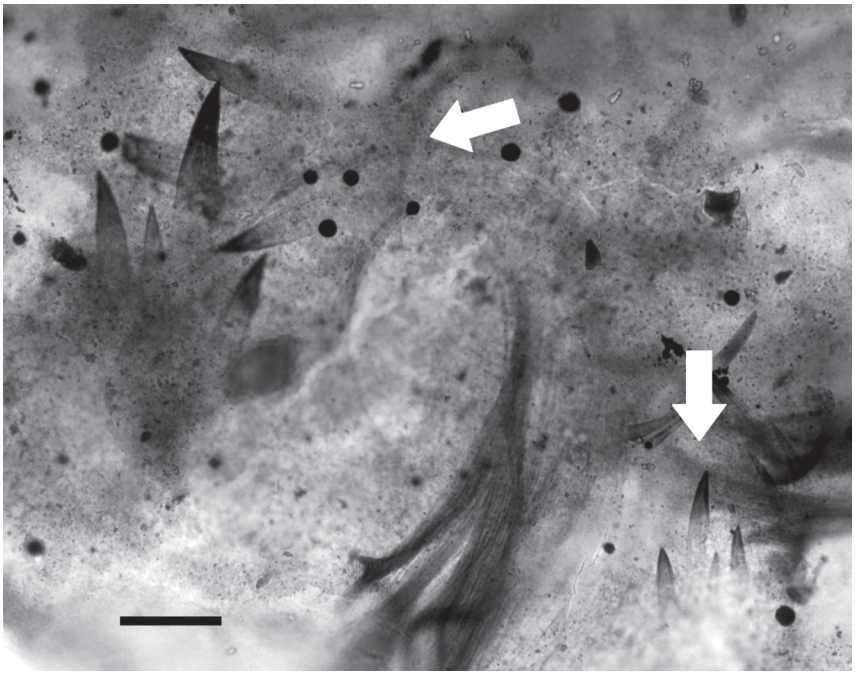

Fig. 5. Different sizes of fossil chaoborid mandibles, found in one coprolite. Transmitted-light microscopy. Scale bar 50 µm.

Figure 8A shows a structure with reticulate wall patterns and a short appendix. These remains are found moderately often in 25 to 50% of the coprolites. They are often associated with pairs of compound eyes and tarsal claws. Comparison with extant structures (Fig. 8B) shows that these are parts of the respiratory horns of chaoborid pupae which were identified by Richter and Wedmann (2005). Their frequency is rather high when it is considered that especially the fourth larval instars are subject to such a strong predation pressure that only a fractional amount of them gets around to pupation (Irvine 1995). Pupal organs are markers of a short period in the life cycle of chaoborid midges. The duration of metamorphosis of tropical *Chaoborus* species is two to a maximum of four days, and, in extant tropical lakes, one complete life cycle including four larval instars and the pupa generally takes about two months (MacDonald 1956; Cressa & Lewis 1986; Irvine 1995). It was found in extant tropical lakes that the larval stages of each *Chaoborus* species form two separate size-groups (MacDonald 1956). Larvae of one generation develop into pupae within a two-week period (Irvine 1995). Pupation and emergence of adult chaoborids in the tropics are synchronised and seemingly associated with the period of the new moon. So, in the tropics, roughly synchronised emergences occur at monthly intervals (MacDonald 1956; Irvine 1997). Possibly a scenario like this can be transferred to the former Lake Messel.

The abundance of phantom-midge structures in the coprolites shows that both larvae and pupae were present in large quantities and were an important component in the food web of Lake Messel. In many extant lakes, chaoborids play a major ecological role in the pelagic food web, as demonstrated, for example, by Carpenter and Kitchell (1993) for some lakes in Wisconsin, USA, and Menz (1995) for Lake Malawi, Africa.

The larvae of phantom midges float in the pelagic zone of a lake. They are translucent and, except for their two pairs of hydrostatic tracheal sacs, almost invisible while motionless.

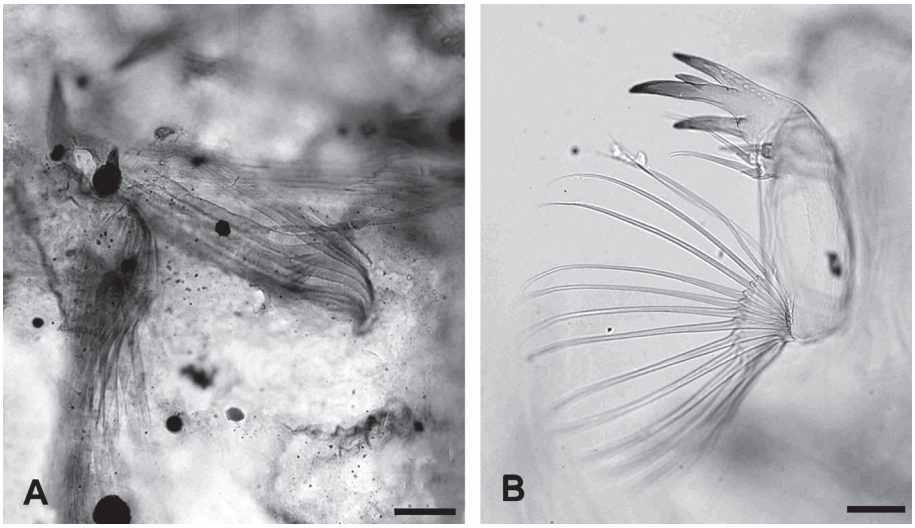

Fig. 6. Mandibles of phantom midge larvae (Chaoboridae): (A) fossil structure in a coprolite; (B) mandible from extant *Chaoborus* sp. Transmitted light microscopy. Scale bar 25 µm in Fig. 6A and 100 µm in Fig. 6B.

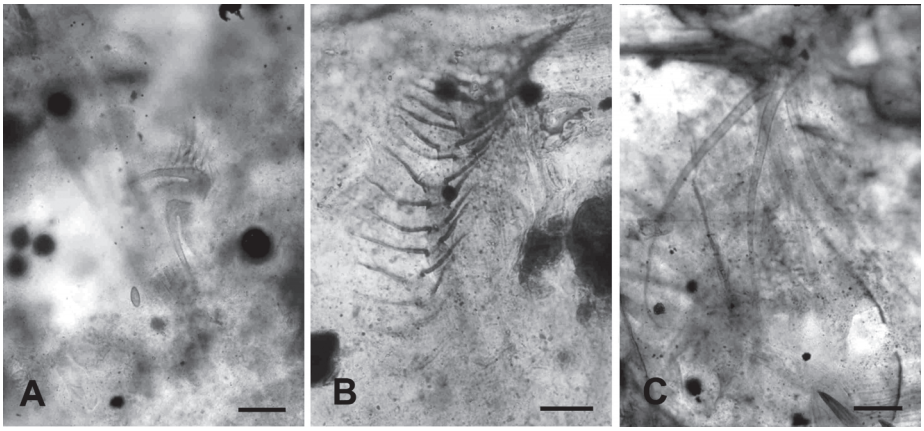

Fig. 7. Fossil structures: (A) pair of caudal hooks, remains of a chaoborid larva; (B) T-shaped bases of setae of an anal fan, remains of a culicoid larva; (C) paddle with supporting midrib, remains of a *Chaoborus* pupa. Transmitted-light microscopy. Scale bars 25 µm.

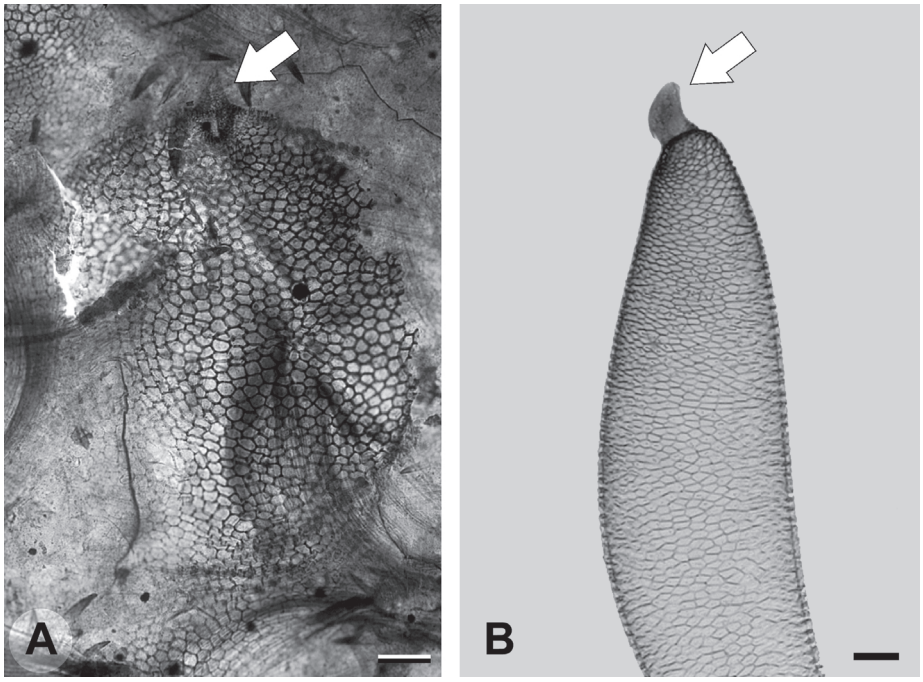

Fig. 8. Parts of respiratory horns of phantom midge pupae (Chaoboridae): (A) upper part of fossil respiratory horn in a coprolite; (B) upper part of a respiratory horn from extant *Chaoborus* sp. The appendices of the respiratory horns are arrowed. Transmitted-light microscopy. Scale bars 50 µm.

Their altered antennae together with the strong mandibles serve for capturing their prey (Fig. 9A). The pupae hover in an upright position in the water (Fig. 9B).

Chaoborid larvae are important both as prey for planktivorous fish and as predators. Diet studies of tropical *Chaoborus* larvae show that the older larval instars feed mainly on small planktonic crustaceans, such as copepods or waterfleas, and only occasionally ingest phytoplankton (Lewis 1975; Moore *et al.* 1994; Irvine 1997). This implies that large populations of chaoborids might have a measurable effect on zooplankton population dynamics (Cressa & Lewis 1986; Lehman *et al.* 1998). Small roundish clusters of phytoplankton are found regularly in the coprolites. These particles may well represent gut contents of prey animals. Moore *et al.* (1994) pointed out that, when present in high density, phytoplankton forms a substantial part of the diet of *Chaoborus* larvae. It is obvious from our study that *Thaumaturus intermedius* from Messel preyed heavily on these larvae. Studies on the food consumption of fish in Lake Malawi show that these insects are an important part of the diet of several pelagic fish species in extant lakes with large chaoborid populations (Allison *et al.* 1995). The possible importance of chaoborids as prey for fish is also shown by He *et al.* (1993).

The presence of these immature stages of chaoborid midges prompts different interesting hypotheses on the former lake ecology. Studies on extant populations of chaoborid larvae in both temperate and tropical lakes show that when planktivorous fish are present, a vertical diurnal migration of the third and fourth larval instars generally occurs (e.g. Sardella & Carter 1983; Irvine 1997). During the night the later instars of chaoborid larvae stay in the upper horizons of the lake to capture their prey (Fig. 10). During the day, in meromictic lakes the chaoborid larvae stay in the upper anoxic horizons of the monimolimnion, where they take refuge from planktivorous fish (Sardella & Carter 1983). A refuge with low oxygen concentration might be essential for the stable presence of high numbers of phantom midge larvae in lakes where they coexist with fish (Irvine 1997).

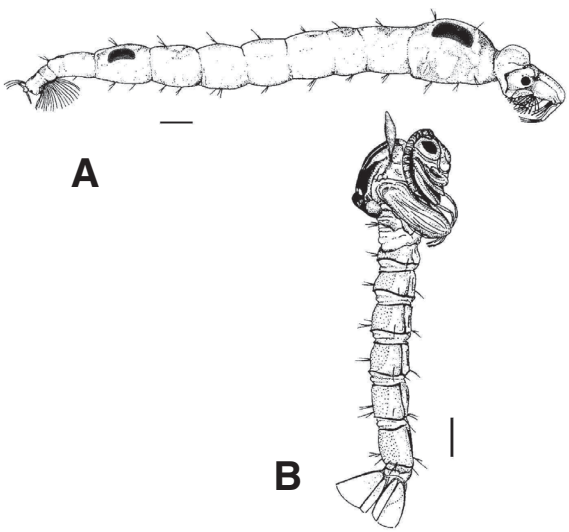

Fig. 9. Immature stages of extant *Chaoborus* sp. in lateral view: (A) larva; (B) pupa. Scale bars 1 mm. Drawings modified after Sæther (1997).

Moreover, Rahel and Nutzman (1994) found that planktivorous fish in extant meromictic lakes venture during the day into the anoxic water zone in search of prey. One can only speculate whether the fossil *Thaumaturus* species in Messel displayed the same behaviour or whether the *Chaoborus* species had no migration behaviour at all.

The investigation of coprolites has confirmed the presence of a great variety of invertebrate organisms in the limnic food web of Lake Messel (Richter & Baszio 2001*a*, 2002). Without analysis of the small fish coprolites, the detection of significant populations of phantom midge larvae would not have been possible. Analysis of the drilling core confirmed the stable presence of *Chaoborus* populations throughout the life span of the former Lake Messel (Richter & Wedmann 2005).

Large populations of immature chaoborid midges also played an important role in other fossil ecosystems. Sinitshenkova (2002) and Zherikhin and Sinitshenkova (2002) gave an overview of assemblages of aquatic insects in lacustrine deposits through time and they distinguished between different assemblage types. Immature stages of chaoborids are preserved, sometimes in huge numbers, in many Mesozoic lakes in Siberia, Mongolia and China. For example, fossils of Chaoboridae are moderately abundant in Lower Jurassic to Lower Cretaceous sediments of several former lakes in Transbaikalia (type A of Sinichenkova & Zherikhin 1996; Jurassic assemblage 2 of Sinitshenkova 2002). In numerous Lower Cretaceous lacustrine deposits from Siberia, Mongolia and China, Chaoboridae are very abundant (types C, D, and E of Sinichenkova & Zherikhin 1996; Cretaceous assemblage types 3, 4, 5, 7, and 8 of Sinitshenkova 2002). Their diversity in these deposits was generally low, with usually only one species occurring in each locality (Sinitshenkova 2002). Immature chaoborids are also quite common in the Lower Cretaceous Koonwarra fossil beds of Australia (Jell & Duncan 1986). Chaoborids and other autochthonous aquatic insects seem to be lacking in Upper

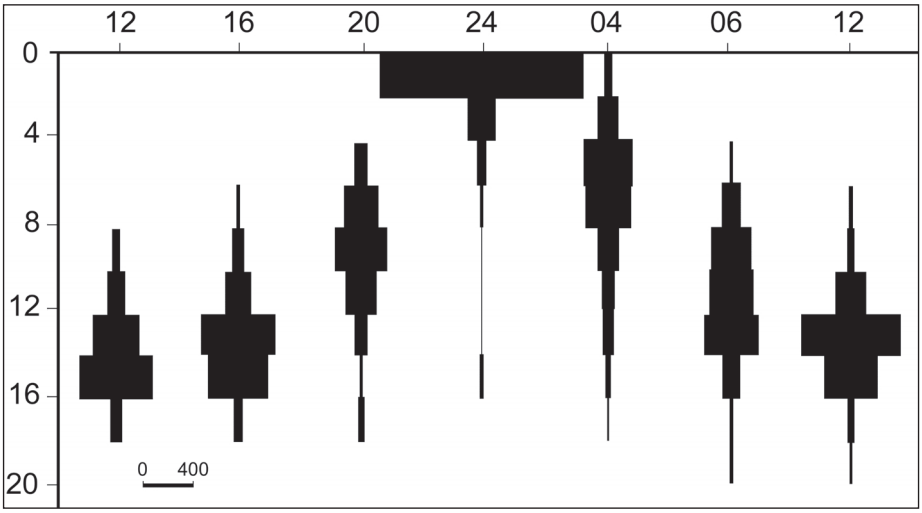

Fig. 10. Vertical diurnal migration of the last larval instar of *Chaoborus punctipennis* in the extant meromictic Crawford Lake, Canada. Crawford Lake is continuously anoxic below 14 m, but the anaerobic boundary may vary seasonally from 11 to 14 m. The hours are plotted horizontally, the depth in metres is plotted vertically. Horizontal scale shows number of individuals/m^3. Modified after Sardella and Carter (1983).

Cretaceous deposits. This is interpreted as that an extinction event of insects which inhabit stagnant water habitats possibly occurred at the end of the Early Cretaceous (Sinitshenkova 2002). Abundant fossils of chaoborid pupae from Cainozoic deposits have been reported by Johnston and Borkent (1998) from the Middle Eocene Tallahatta Formation in Mississippi, USA.

These examples show that lakes with large populations of chaoborid midges existed for a long time. A major difference between all these deposits and Messel is that in all the other deposits body fossils of chaoborids have been found, whereas in Messel the presence of chaoborids is proven almost only via investigation of fish coprolites. Only after close examination some seemingly isolated mandibles of the larvae were also found directly in the sediment. The lack of complete body fossils is possibly due to very weak sclerotisation of the larvae. It is likely that the larvae are preserved in the sediment but cannot be seen because of their translucent body. The lack of body fossils of adult chaoborid midges shows the importance of taphonomic influences on the taxonomic composition of fossil assemblages. In general, body fossils of dipterans (midges and flies) are very rare among thousands of insect fossils from Messel.

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A new fossil oonopid spider in lowermost Eocene amber from the Paris Basin, with comments on the fossil spider assemblage

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ABSTRACT

A new spider species from the family Oonopidae is described from lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France. *Orchestina parisiensis* sp. n. is the first spider to be described from French amber. Preliminary observations on the fossil spider assemblage support a warm climate in this region during the lowermost Eocene. A remarkable feature of this deposit is the absence of jumping spiders (Salticidae) as amber inclusions, because they are frequent in other Tertiary fossil resins. Thus, this new amber deposit may hold vital clues relating to the historical biogeography of the Salticidae, the most diverse spider family on the planet today.

KEY WORDS: Araneae, Haplogynae, Oonopidae, *Orchestina*, French amber, new species.

INTRODUCTION

The family Oonopidae consists of ecribellate, haplogyne spiders less than 3 mm in body length, which have a wide geographical distribution, particularly in the tropics. There are 459 extant species in 67 genera (Platnick 2005). Oonopids are fast-moving, nocturnal hunters that actively pursue their prey and they are often encountered as fossils preserved in amber. Despite being unknown as fossils in sediments, the Oonopidae are known from more fossil deposits than any other spider family and were already widespread by the Cretaceous (Penney 2006). The family also contains the oldest example of an extant spider genus. Their small size, wandering behaviour and widespread distribution may account for their frequent occurrence as amber inclusions, because amber tends to be biased towards trapping wandering, active hunters, rather than sedentary spiders (Penney 2002). For comprehensive reviews of fossil Oonopidae see Wunderlich (1981, 2004) and Penney (2000, 2006).

France has a rich and diverse fossil spider fauna, with both the oldest known mesothele (Selden 1996) and mygalomorph (Selden & Gall 1992) spiders originating from French sediments. Early reports of French fossil spiders include those of Gourret (1888) and Berland (1939) who described araneomorph Tertiary fossil spiders in sediments from Aix en Provence. Spiders in Cretaceous ambers from France have been known for some time (e.g. Schlüter 1978; Néraudeau *et al*. 2002) but these have yet to be described. Recently, Nel *et al*. (2004) identified a new source of undescribed fossil amber spiders from the lowermost Eocene of Le Quesnoy in the Paris Basin and the presence of Oonopidae from this deposit was reported by Penney (2006, text-fig. 2).

The amber-bearing strata occur under the River Oise Quaternary deposits. They prograde toward the north-east and lie at the bottom of two channels, which cut into the underlying Thanetian marine greensands. The Sparnacian beds consist of a succession of lenticular bodies with two main facies. Firstly, clayed sands rich in frequently pyritised lignite, together with amber, and secondly, grey clayey sands with less lignite and with a continental vertebrate fauna (Nel *et al.* 2004). The first reconstruction of the palaeoenvironment was provided by Nel *et al.* (1999) and summarised by Nel *et al.*

(2004). Based upon the fossils identified to date, Nel *et al.* (2004) concluded that some 53 Myr ago the region consisted of a wet river forest surrounded by semi-deciduous or deciduous woodland, in a warm climate with wet and dry seasons.

Inroads have been made with regard to the insect inclusions from the Paris amber (see the various papers in Nel 2004), but spiders have not hitherto been described. A recent research visit to the Muséum National d'Histoire Naturelle in Paris yielded new fossil spiders from this amber deposit. As with most ambers, many of the spiders were juvenile and unidentifiable and most of the adult specimens are still undergoing preparation in Paris. However, one new species was identifiable and this is described herein and preliminary observations on the fossil spider assemblage are provided.

MATERIAL AND METHODS

The specimens upon which this paper is based are deposited in the Muséum National d'Histoire Naturelle (MNHN), Paris, France. All measurements were made using an ocular graticule and photographs were taken with a Nikon D1X digital camera attached to a Wild M8 stereomicroscope.

TAXONOMY

Order Araneae Clerck, 1757
Suborder Opisthothelae Pocock, 1892
Infraorder Araneomorphae Smith, 1902
Family Oonopidae Simon, 1890

Genus *Orchestina* Simon, 1882

Type species: *Schoenobates pavesii* Simon, 1873, by monotypy; Recent, Spain, southern France, Corsica, Algeria.

Remarks: This genus is known from 36 extant species and has a global distribution, primarily in warmer regions (Platnick 2005). Fossils are known in ambers from the Dominican Republic (two species; Wunderlich 1981, 1988), the Baltic region (11 species; Wunderlich 2004), China (one species; Wunderlich 2004), Mexico (one species; Petrunkevitch 1971), Rovno (undescribed; Wunderlich 2004), Canada (one species; Penney 2006), Myanmar (one unnamed specimen; Penney 2006), New Jersey (one unnamed specimen; Penney 2004), Álava (pers. observ.) and copals from Madagascar (one species; Wunderlich 2004), Kenya (two species; Wunderlich 1981) and Colombia (two species; Wunderlich 2004). Extant species are active hunters that jump frequently (Wunderlich 2004), presumably facilitated by their thickened fourth femora.

Orchestina parisiensis sp. n.

Fig. 1

Etymology: After the type locality.

Diagnosis: The main diagnostic characters of male *Orchestina* are the relative proportions of the palpal segments and the shape of the embolus (Wunderlich 2004). The bifid tip of the embolus and the embolus length relative to that of the bulb distinguish the new species.

Description (based primarily on holotype): Body length approximately 1.0 mm; carapace 0.54 mm long, 0.43 mm wide, domed and without the long, erect setae often observed

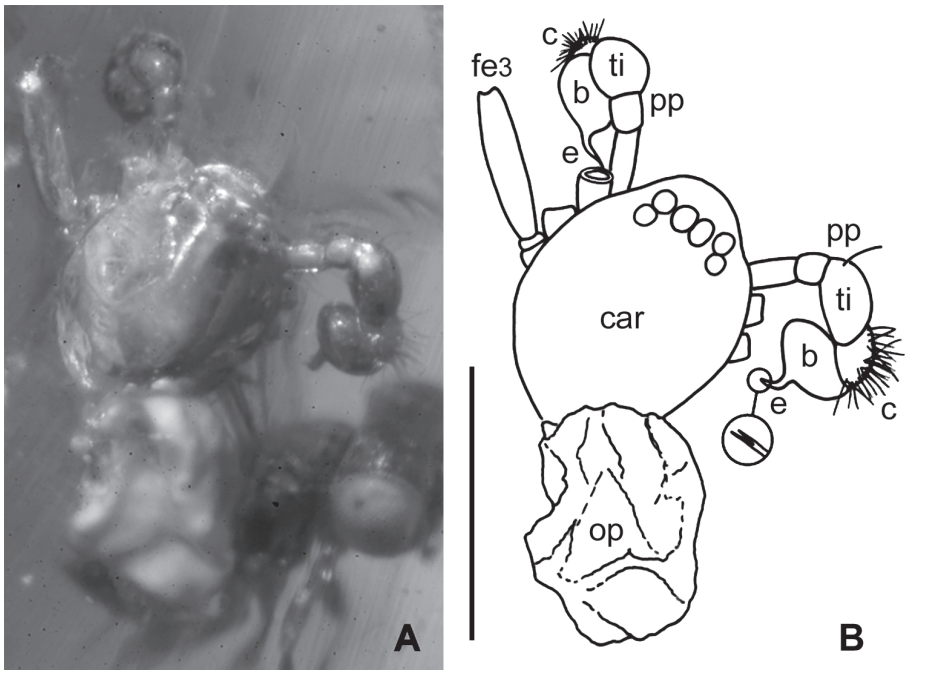

Fig. 1. *Orchestina parisiensis* sp. n., holotype PA 759 (lowermost Eocene amber from Le Quesnoy, Paris Basin, France): (A) dorsal view of the specimen in amber, (B) details of the body structures, dorsal view. Abbreviations: (b) bulb, (c) cymbium, (car) carapace, (e) embolus, (fe) femur, (op) opisthosoma, (pp) pedipalp, (ti) tibia. Scale bar 0.5 mm.

in other fossil *Orchestina*. Six eyes in the segestroid position (*sensu* Wunderlich 2004) typical of the genus. Opisthosoma approximately 0.5 mm long, 0.4 mm wide. Femur of leg 4 (as seen in the paratype) distinctly larger than legs 1–3; all legs without spines. The pedipalp is clearly visible in the holotype: tibia 0.16 mm long, 0.10 mm high, the cymbium is small and highly setose, bulb subspherical, 0.17 mm wide, 0.11 mm high; embolus 0.07 mm long with a kink distally and with a bifid tip (Fig. 1B).

Holotype: PA 759, male, visible in dorsal view, opisthosoma collapsed and covered with a white emulsion as commonly observed in Baltic amber inclusions, spinnerets not visible, only third left leg present and only femur and patella can be seen but are not in a position conducive to taking measurements; there is one cyclorraphan fly syninclusion preserved directly below the holotype. FRANCE: *Oise*: Paris Basin, Le Quesnoy; lowermost Eocene amber.

Paratype: PA 1909, male, same data as the holotype.

Remarks: This is the first spider species to be described from French amber. Based on the palpal structure and particularly the bifid tip of the embolus, the new species is probably most closely related to *O. baltica* Petrunkevitch, 1942 (see Wunderlich 1981, fig. 4, 2004, figs 8k–m). However, the embolus of *O. baltica* is longer than the height of the bulb, whereas that of the new species is shorter. The holotype was selected based on the exceptional view of the pedipalp (the most important structure for species identification in spiders). However, in this specimen the fourth pair of legs is missing, but these are preserved in the paratype and have the thickened femur diagnostic of the genus *Orchestina*.

DISCUSSION

All insect species described from this deposit to date (see Nel *et al.* 2004), and the spider described here, are new to science. Nel *et al.* (2004) considered the fauna to be unique to the Paleocene/Eocene of Western Europe. In addition, from an entomological perspective this fauna appears to have few genera in common with that of the Upper Eocene–Lower Oligocene Baltic amber. The species described above and preliminary observations of additional material suggest that this will not necessarily be the case for the spider fauna, with both deposits sharing numerous genera. However, clarification of this will have to wait until the material in the MNHN has been suitably prepared for systematic study. The spider families provisionally identified to date include: Oonopidae, Theridiidae, Hersiliidae, Segestriidae, Archaeidae, Uloboridae, Pholcidae, Anapidae *s.l.*, ?Tetragnathidae, ?Agelenidae and Selenopidae. This assemblage is characteristic of a warm, sub-tropical environment, supporting the palaeoenvironmental conclusions of Nel *et al.* (1999, 2004).

One remarkable feature of this deposit is the absence of jumping spiders (Salticidae) as amber inclusions. Extant salticids have a global distribution and are the most diverse spider family on the planet today, with more than 5000 recognised species in 550 genera (Platnick 2005). They are highly distinctive as a result of their large anterior median eyes, and can be easily identified even from very tiny juvenile specimens. Thus, they were not accidentally overlooked in the 230+ specimens examined by the author. They occur frequently as Tertiary fossils in ambers from the Baltic region (e.g. Petrunkevitch 1958) and the Dominican Republic (e.g. Penney & Pérez-Gelabert 2002). However, no salticids have been described from Cretaceous deposits. The specimen listed as a salticid in New Jersey amber by Grimaldi *et al.* (2002) and the specimen figured as Salticidae by Néraudeau *et al.* (2002) from Cretaceous amber of France were misidentifications (pers. observ.). It is evident that many extant spider families have a long geological history (Penney *et al.* 2003) and the active, predatory behaviour of salticids predisposes them to becoming trapped in resin (Penney 2002). Therefore, Salticidae may be a recently evolved family and previously their niche may have been occupied by an extinct spider family, such as the Lagonomegopidae (e.g. Eskov & Wunderlich 1995).

The absence of Salticidae in this deposit is a sufficient cause to question the Tertiary age of this amber. However, the absence of the strictly fossil family Lagonomegopidae, which is relatively common in Cretaceous ambers (e.g. Penney 2005) supports a Tertiary age for this deposit. The absence of Salticidae is certainly enigmatic and this new amber deposit may hold vital clues relating to the historical biogeography of the most diverse spider family on the planet today.

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An enigmatic Palaeozoic stem-group: Paoliida, designation of new taxa from the Upper Carboniferous of the Czech Republic (Insecta: Paoliidae, Katerinkidae fam. n.)

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ABSTRACT

Two new representatives of stem group Paoliida are described and illustrated from the Upper Carboniferous of the Upper Silesian Coal Basin (Czech Republic), i.e. *Katerinka hilaris* gen. et sp. n. (Katerinkidae fam. n.) and a further fragmentary specimen with uncertain familial attribution (?Paoliidae). Rediscovery of the missing holotype specimen *Holasicia sustai* Kukalová, 1958 enabled detailed study and description of the monotypic genus *Mertovia* gen. n., type species *Mertovia sustai* (Kukalová, 1958), comb. n. (Paoliidae). The material was classified and compared with all possibly related taxa on the basis of the wing venation. Some uncertainties on the current state of knowledge of certain taxa with similar wing-venation pattern and their systematic attribution were considered. The fossil record of Paoliidae is briefly discussed and a check-list is provided.

KEY WORDS: Paoliida, Paoliidae, Katerinkidae, Palaeozoic, Upper Carboniferous, Namurian, Westphalian A (Langsettian), Upper Silesian Coal Basin, Czech Republic, new taxa.

INTRODUCTION

The order Paoliida Handlirsch, 1906 (= Protoptera Sharov, 1966) is small group of pterygote insects with eight described genera and ten species known from a relatively short period in the Upper Carboniferous (Namurian B to Westphalian A (= Langsettian)). Paoliids were probably restricted to the territory within the Laurasian continent according to their presence in deposits of North America (East USA) and Europe (Belgium, Czech Republic, England, Germany, The Netherlands, Wales) (see Fig. 1). The difficulties with definitive assessment of particular extinct higher taxa based on fragmentary fossils were shown by Hennig (1981: 148) who traced paoliids as an interesting example.

Systematic attribution of the family Paoliidae within the order Palaeodictyoptera was primary established by Handlirsch (1906) who proposed a close relationship with spillapterids. He placed Scudder's two species into this new family on the basis of the spread-out and copious branching of the cubital and anal veins along the inner margin of the wing (Handlirsch 1906). Before that Brongniart (1883: 160) had assigned *Paolia vetusta* Smith, 1871 to protolocustids and on the contrary Scudder (1885*a*, *b*) attributed *Paolia vetusta* Smith, 1871 and ?*Paolia gurlei* Scudder, 1885 to protophasmids. At a later stage, Kukalová (1958*a*) in her extensive work on new taxa from the Upper Silesian Coal Basin, integrated this family as a group of 'Protorthoptera' (Cacurgoidea). Sharov (in Rodendorf 1962) first considered Paoliidae within 'Paraplecoptera' and subsequently included them in 'Archaeoptera', as a basal stem group of Pterygota (Sharov 1966). Carpenter (1992) placed Paoliidae within the most primitive Protorthoptera together with Homoeodictyidae and Thoronysididae, since these families have reticulate venation (so-called 'archedictyon') as well as a concave MP in the forewing. Further re-

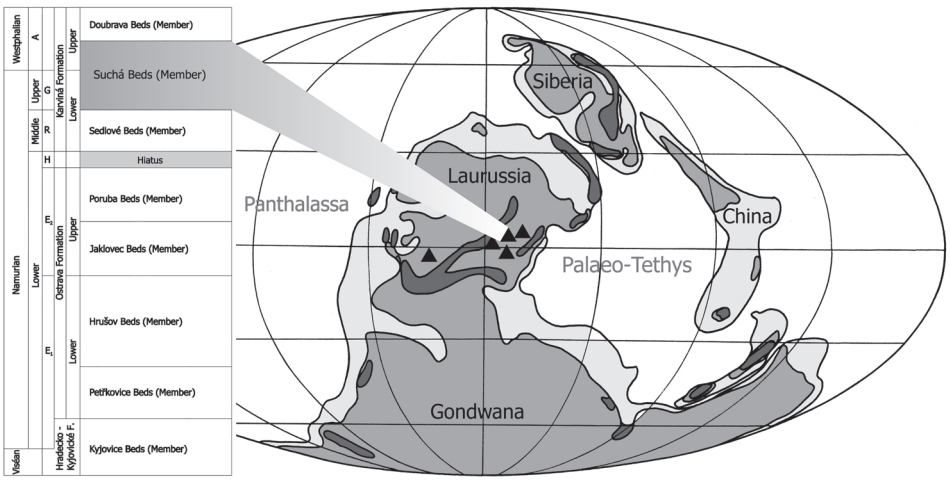


Fig. 1. Location of the Upper Silesian Coal Basin (Czech Republic) within Upper Carboniferous palaeogeographical world map and stratigraphical position in lithostratigraphic division of the Carboniferous in the Upper Silesian Coal Basin the Czech Republic after Dopita *et al*. (1997, modified). Proximate distribution of other paoliid species within palaeogeographical world map indicated by black triangles (palaeogeographical map after Scotese (2005), modified).

arrangement into the 'hemipteroid lineage' was done by Kukalová-Peck and Brauckmann (1992) based on the presence of an 'arculus' between veins MP and CuA and simultaneously a simple CuP or only terminal twigging. Finally Rasnitsyn (Rasnitsyn 1976; Rasnitsyn & Quicke 2002, fig. 1) considered paoliids as a basal stem group of the Pterygote lineage as was proposed by Sharov (1966), but without any distinct synapomophies.

The Upper Silesian Basin (USB) is a triangular sedimentary structure situated partly in the NE of Moravia (Czech Republic) and mainly in the Silesian part of Poland (see Dopita *et al.* 1997: 34). From a palaeogeographical point of view, it is similar to the coal basins of the European Variscides from Wales through Belgium to northern Germany. These basins form part of the Subvariscicum. The USB was formed as a top molasse stage of the polytypic foreland basin (Dopita *et al*. 1997). The basin is filled with Lower and Upper Carboniferous continental and marine sediments divided into three main lithostratigraphical units (Hradecko-Kyjovické Formation, Ostrava Formation, Karviná Formation) in the Czech region (see Fig. 1). Zoopalaeontological and phytopalaeontological records were extensively reviewed by Řehoř and Řehořová (1972) and Dopita *et al*. (1997). Fossil insects were found almost entirely from the Karviná Formation (Suchá Beds Member) described by Kukalová (1958*a*, *b*, 1959, 1960, 1964). Recently, a single specimen attributed within Archaeorthoptera was discovered from the drilling core in the basal part of the Ostrava Formation (Petřkovice Beds Member) and published by Prokop *et al*. (2005).

MATERIAL AND METHODS

The material was kept in a dry state without further fixation and deposited in the palaeontological collection of the Municipal Museum in Ostrava (Czech Republic). Standard techniques of observation under a stereomicroscope (Olympus SZX 9/12)

and digital photography (Olympus 5060, Nikon 4500) were employed to examine the material in the dry state or under ethyl alcohol. The classical preparation technique was applied.

We follow the wing-venation nomenclature of Kukalová-Peck and Brauckmann (1992).

TAXONOMY

Order Paoliida Handlirsch, 1906
Family Paoliidae Handlirsch, 1906

Type genus: *Paolia* Smith, 1871.

List of included genera, after Carpenter (1992) and Brauckmann (1984) and reviewed by Rasnitsyn (Rasnitsyn & Quicke 2002): *Holasicia* Kukalová, 1958; *Kemperala* Brauckmann, 1984; *Olinka* Kukalová, 1958; *Paolia* Smith, 1871; *Paoliola* Handlirsch, 1919; *Pseudofouquea* Handlirsch, 1906; *Sustaia* Kukalová, 1958; *Zdenekia* Kukalová, 1958 (see Appendix).

Genus **Mertovia** gen. n.

Etymology: Named after E. Mertová, curator of palaeontology in Municipal Museum in Ostrava; feminine gender.

Type species: *Holasicia sustai* Kukalová, 1958, by present designation.

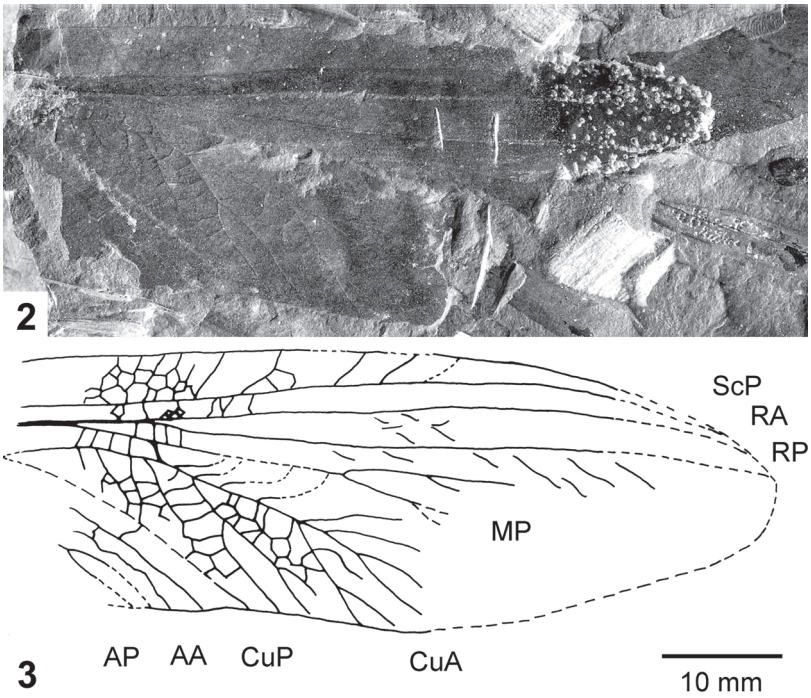
Diagnosis: Based on fore-wing venation, *Mertovia* gen. n. differs from all other paoliid genera by the following combination of characters: ScP ending on costal margin a little above wing apex; RA simple and straight, probably ending well before wing apex; RP parallel to RA and simple, without clear distal branches, probably reaching wing margin at wing apex (estimated from the fragment); MP with a neutral convexity, divided into two (maybe three) posterior branches in its distal half; a very strong convex 'arculus' between CuA and MP just opposite the fork of RA and RP; CuA convex, with 5 or 6 posterior branches ending in CuP or in posterior wing margin; simple CuP strongly concave; three convex anal veins.

Mertovia sustai (Kukalová, 1958), **comb. n.**

Figs 2, 3

Protoblatoid sp. (Cacurgidae): Šusta 1928: 414, pl. 17, fig. 8.
Holasicia sustai: Kukalová 1958: 943, fig. 4.

Redescription: Distal two-thirds of fore wing with dark coloration, no spot or other colour pattern, with clearly visible reticulate venation (so-called 'archaedictyon') and rather thick membrane; fragment 52 mm long, probable complete length about 75 mm, maximum width 24 mm; area between C and ScP 4.4 mm wide, with net of small cells and veinlets in basal half and 4 or 5 weak branches of ScP in distal half; ScP clearly concave, ending on costal margin a little above wing apex; RA convex, straight and simple, with no branches, probably ending well before wing apex; RP diverging from R about 54.4 mm from wing apex, basally with neutral convexity and clearly concave in its distal half, with net of veinlets between it and RA and between it and M; RP simple, without clear distal branches, parallel to RA, probably reaching wing margin at wing apex; base of M poorly preserved, with convex MA between M and R not visible; MP



Figs 2, 3. *Mertovia sustai* (Kukalová, 1958), comb. n. (Paoliidae), photograph and line drawing of holotype specimen B13189, collection of the Municipal Museum of Ostrava.

with neutral convexity, divided into two (maybe three) posterior branches in its distal half; very strong convex 'arculus' between CuA and MP, about 53.5 mm from wing apex, opposite base of RP; CuA convex, with 5 or 6 posterior branches ending in CuP or in posterior wing margin; several oblique veinlets between CuA and MP and three anterior branches emerging from CuA distally, with apparent trichotomy between first anterior branch of CuA, main CuA and posterior branch of CuA; point of separation between CuA and CuP not preserved, but very basal; CuP strongly concave; three convex anal veins partly visible.

Holotype: specimen B13189, imprint of the distal two-thirds of well preserved fore wing (originally Šusta coll.). CZECH REPUBLIC: Upper Silesian Coal Basin, Hlubiná Pit in Karviná, hanging wall seam (No. 24); Upper Carboniferous, Westphalian A (Langsettian), Upper Suchá Beds (Member), Karviná Formation.

Discussion: The description of *H. sustai* was originally based only on a photograph of '*Protoblatoid* sp.' from Šusta's work (1928: 414, pl. XVII, fig. 8), because at that time it was impossible to locate the specimen within the collection. Nevertheless, Kukalová believed that one day it could be recovered in the collection of the Municipal Museum in Ostrava. Subsequently, the missing holotype specimen did reappear during the transfer of the collection to another site. This rediscovery enabled a detailed study of the wing venation (Figs 2, 3) and subsequent redescription.

The organisation of the median vein with a strong convex veinlet (arculus) between it and a clearly convex cubital vein, together with the absence of a developed convex vein MA corresponds to the 'paoliid line' pattern of wing venation of Kukalová-Peck

and Brauckmann (1992, fig. 41). Such a convex arculus is also present in some taxa currently included in the Grylloblattodea, but they have a well developed convex MA, unlike this fossil. Those authors included the following families in the 'paoliid line': Paoliidae Handlirsch, 1906, Eucaenidae Handlirsch, 1906, Strephocladidae Martynov, 1938, Blattinopsidae Bolton, 1925, Synomaloptilidae Martynov, 1938, and Cymbopsidae Kukalová, 1965. Among these families, the Eucaenidae, Blattinopsidae, Strephocladidae, and Cymbopsidae strongly differ from *Mertovia* in their RP with numerous posterior branches. Carpenter (1992) included the Synomaloptilidae in the order Caloneurodea Handlirsch, 1937 but Béthoux *et al*. (2004) excluded them from this order. Rasnitsyn (Rasnitsyn & Quicke 2002) transferred them to the superorder Hypoperlidea Martynov, 1928. The medio-cubital pattern of *Synomaloptila* Martynov, 1938 remains poorly known but it differs from *Mertovia* in its cubital vein (CuA?) with only two distal branches (Carpenter 1992, fig. 128.1; Rasnitsyn & Quicke 2002, fig. 121).

Kukalová-Peck and Brauckmann (1992) added *Limburgina* Laurentiaux, 1950, but Béthoux and Nel (2002) noted that it is impossible to attribute it to the 'paoliid line' or to the Archeorthoptera Béthoux & Nel, 2002. The radial area of *Mertovia* is completely different from that of *Limburgina*. Kukalová-Peck and Brauckmann (1992) also included *Heterologopsis* in the 'paoliid line' but Béthoux and Nel (2002) demonstrated that it is an Archeorthoptera.

Rasnitsyn (Rasnitsyn & Quicke 2002) considered the Paoliidae to be the most inclusive group of the Pterygota, and as a unique family of the order Paoliida. Thus he did not follow the hypothesis of Kukalová-Peck and Brauckmann (1992) and considered the 'arculus' *sensu* Kukalová-Peck and Brauckmann (1992) as a very short vein M5. He also indicated that the Paoliida have no synapomorphies, which makes the characterisation of this order particularly difficult. Therefore, the phylogenetic relationships of the Paoliidae remain controversial and unresolved. Nevertheless, the wing venation of *Mertovia* is very similar to those of some Paoliidae like *Zdenekia* or *Paolia*, at least in the organisation of the cubito-median veins and the long RP with few apical branches.

Rasnitsyn (Rasnitsyn & Quicke 2002) included eight genera in the Paoliidae. *Zdenekia* shares with *Mertovia* a ScP separated from RA, but it is distinctly shorter, not reaching the wing apex, and unlike *Mertovia* its RP has three distal posterior branches (Kukalová 1958, text-fig. 1). The ScP of *Holasicia*, *Pseudofouquea*, *Paoliola*, *Olinka*, and *Paolia* ends in RA and the RP has numerous posterior branches (Melander 1903; Kukalová 1958, text-figs 3, 5, 9–12; Maples 1989, 1991). *Kemperala* also has a ScP ending in RA, but the RP in its fore wing is apparently simple and vanishes in the area between RA and M (Brauckmann 1984; Brauckmann *et al*. 1985).

Unlike *Mertovia*, *Sustaia* has a ScP ending in RA, but even if its RP is poorly preserved, it has no posterior branches in nearly all its length, as in *Mertovia* (Kukalová 1958, text-fig. 6, pl. 2, fig. 1). Another difference is the presence of numerous small branches of the anal vein in *Sustaia*, which is not apparent in *Mertovia*.

Carpenter (1992) considered the genus *Paolekia* Riek, 1976, originally included in the Paoliidae, as a 'Protorthoptera of family uncertain'. The difference between *Paolekia* and *Mertovia* lies in the wing apex, the RP of *Paolekia* having no fewer than four main branches (Riek 1976).

Handlirsch (1911) described the monotypic family Schuchertiellidae on the basis of a very incomplete wing base. Carpenter (1992) considered *Schuchertiella* Handlirsch,

1911 as *incertae sedis*. It has a strong oblique veinlet between a (probable) median vein and a (probable) cubital vein, but nothing is known about the convexity of these veins. Thus, it is not possible to determine if the family Schuchertiellidae belongs to the 'paoliid line' or to the Archaeorthoptera. Nevertheless, it differs from *Mertovia* in its basally forked alleged median and cubital veins.

Family ?Paoliidae Handlirsch, 1906
Genus undetermined

Figs 4, 5

Description: Distal two-thirds of wing uniformly dark, with clearly visible reticulate venation (so-called 'archaedictyon') and rather thick membrane, rather narrow elongate; fragment 31.1 mm long, estimated wing length about 50 mm, maximum width based on fragment 14.5 mm; only apex of concave vein ScP preserved, ending in convex RA, 26.1 mm from wing apex; several veinlets between RA(+ScP) and costal margin; simple RA reaching wing margin 5.5 mm above apex; numerous sigmoidal cross-veins between RA and RP; concave RP divided into two main branches 30 mm from wing apex, anterior branch subdivided into four branches and posterior one into three branches; no convex vein MA; concave vein interpreted as MP divided into two main branches, anterior one divided into three long branches and posterior one divided into two branches; apical parts of other veins CuA, CuP and probably anal veins visible.

Material examined: specimen B13190, part and counterpart of the apical part of a well preserved wing, uniformly dark (originally Šusta coll.). CZECH REPUBLIC: Upper Silesian Coal Basin, František Mine in Horní Suchá, hanging wall seam D (second etage); Upper Carboniferous, Westphalian A (Langsettian), Upper Suchá Beds (Member), Karviná Formation.

Discussion: Because of the absence of the structures of the basal half of the wing, its determination is tentative. Nevertheless, it has the main structures of the distal half of some paoliid wings, viz. apical fusion of ScP with RA, and absence of convex MA between concave RP and MP. This fossil differs from the wing of *Paoliola gurleyi* (Melander, 1903) only in the longer fusion of RA with ScP and longer distal branches of RP (Kukalová 1958). Therefore, we provisionally place it close to the Paoliidae.

Family **Katerinkidae** fam. n.

Type genus: *Katerinka* gen. n.

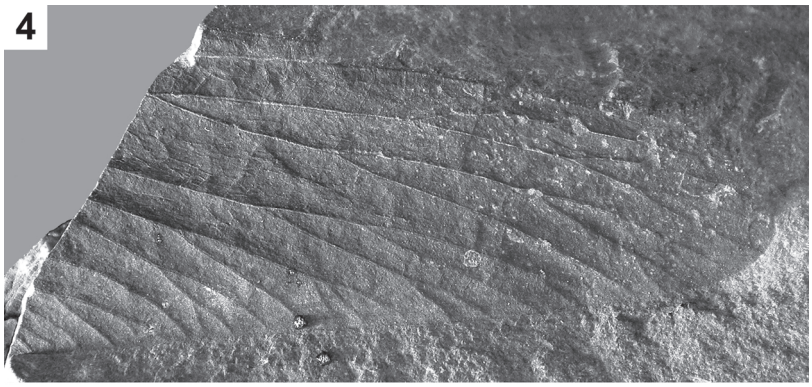
Diagnosis: Wide costal area between RA (+ScP) and C; vein ScP short, ending in RA slightly distad of RP base, in basal half of wing; RA with some anterior branches close to its apex; basal fork of RA/RP; concave RP with few distal branches; concave MP with two main branches rather basal to base of RP; rather pronounced convex 'arculus' between MP and convex CuA, basal to RP origin; area between CuA and CuP with net of veinlets; CuA with five distal posterior branches.

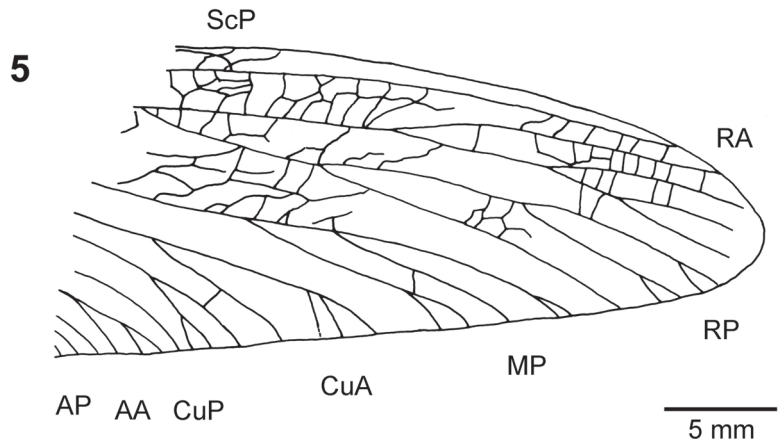
Genus **Katerinka** gen. n.

Etymology: Named after diminutive of Katerina (Katerinka in Czech), JP's daughter.

Type species: *Katerinka hilaris* sp. n., by present designation.

Diagnosis: As for the family.





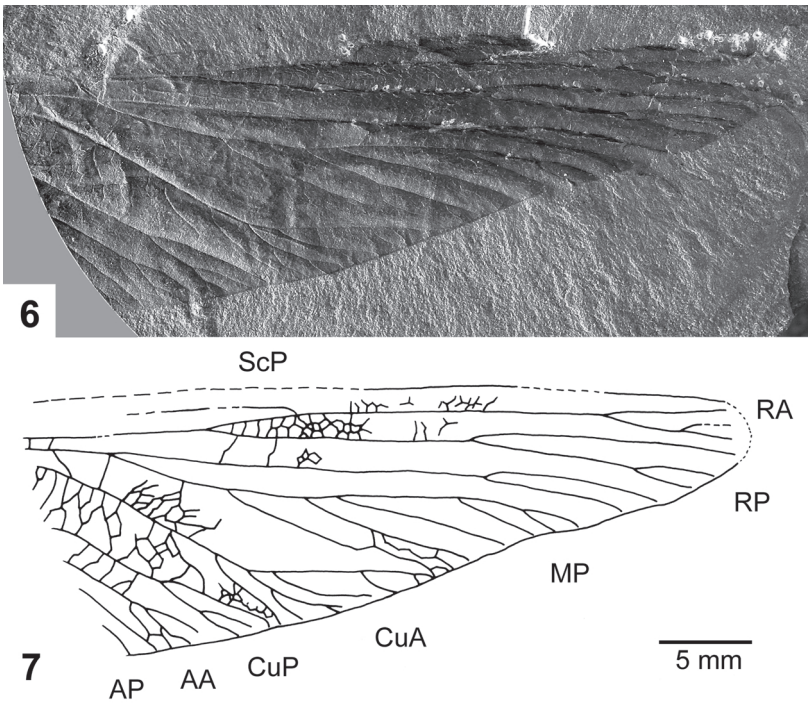
Figs 4, 5. Undetermined genus of presumed Paoliidae, photograph and line drawing of specimen B13190, collection of the Municipal Museum of Ostrava.

Katerinka hilaris sp. n.

Figs 6, 7

Etymology: From Latin *hilaris* (cheerful).

Description: Wing dark in coloration, with clearly visible reticulate venation (so-called "archaedictyon") and rather thick membrane, alternation of main veins not very prominent; wing fragment 40 mm long (estimated length about 50 mm), 15 mm wide (widest part at base of preserved portion); vein ScP rather poorly indicated as faint traces, but distinctly ending in RA only slightly distal of base of RP, very far from wing apex; net of small veinlets in area between C and RA (+ScP); RA convex, with three weak anterior branches near its apex; RA apparently ending near wing apex; RP base 30.2 mm from wing apex; RP concave with two main anterior branches, second terminally twigged; no convex vein MA, rather pronounced convex 'arculus' between concave median vein MP and convex CuA, 8.4 mm basad of RP base; MP divided into two main branches 5.5 mm basal to bifurcation RA and RP; anterior branch of MP straight, apically forked; posterior branch of MP with six posterior branches ending in posterior wing margin; distal part of CuA strongly sigmoidal, with five posterior branches



Figs 6, 7. *Katerinka hilaris* gen. et sp. n. (Katerinkidae fam. n.), photograph and line drawing of holotype specimen B11978, collection of the Municipal Museum of Ostrava.

ending in posterior wing margin but with no clear anterior branches; concave CuP with three apical branches; area between CuA and CuP with net of veinlets; two veins parallel to CuP, probably corresponding to anal veins, first apically forked.

Holotype: specimen B11978 counterpart of well preserved almost complete wing, missing basal part and tip of apex, costal area partly destroyed (originally Horák coll.). CZECH REPUBLIC: Upper Silesian Coal Basin, Doubrava Mine, borehole Cr 92, depth 201.8 m; Upper Carboniferous, Namurian–Westphalian A (Langsettian), absolute age about 315 Ma, Group of Hubert faunistic horizons, Lower–Upper Suchá Beds (Member), Karviná Formation.

Discussion: This fossil has the wing venation pattern of the 'paoliid line' sensu Kukalová-Peck and Brauckmann (1992), with a concave MP, no convex MA between MP and RP, a strong convex 'arculus' between convex CuA and MP, and a concave CuP. It differs from all the families that Kukalová-Peck and Brauckmann (1992) included in the 'paoliid line' in its short ScP ending in RA just distal to base of RP, and wide costal area between RA (+ScP) and C. Therefore we propose a new family for this fossil, probably closely related to the Paoliidae.

CONCLUSIONS

The new data support the hypothesis of favourable living conditions for paoliids within the territory of the Upper Silesian Coal Basin, since five of the eleven world species of paoliids are recorded from this locality (see check-list of Paoliidae in Appendix, Fig. 1). However, this bizarre phenomenon can be explained by insufficient records of

Late Namurian to Langsettian deposits elsewhere, and by a short period of existence of this group. Thus we prefer to retain both separate families, Paoliidae and Katerinkidae fam. n., without any strict relationship until the higher phylogeny of this group is resolved.

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Appendix

Updated check-list of described Paoliidae from Carpenter (1992):

Holasicia vetula Kukalová, 1958	Czech Republic (Upper Silesian Coal Basin)
Holasicia rasnitsyni Brauckmann, 1984	Germany (Hagen-Vorhalle)
Kemperala hagensis Brauckmann, 1984	Germany (Hagen-Vorhalle)
Mertovia sustai (Kukalová, 1958), **comb. n.**	Czech Republic (Upper Silesian Coal Basin)
Paolia vetusta Smith, 1871	USA (Indiana), The Netherlands (Limbourg)
Paoliola gurleyi (Melander, 1903)	USA (Indiana)
Pseudofouquea sp.	England (Bickershaw): Anderson *et al.* 1997
Pseudofouquea cambrensis (Allen, 1901)	Wales (Llanbradach Colliery)
Sustaia impar Kukalová, 1958	Czech Republic (Upper Silesian Coal Basin)
Zdenekia grandis Kukalová, 1958	Czech Republic (Upper Silesian Coal Basin)
Zdenekia occidentalis Laurentinaux, 1986	Belgium (Charbonnages de Ressaix)

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A review of the South American Palaeozoic entomofauna Part I: the Ischnoneuroidea and Cacurgoidea, with description of new taxa

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ABSTRACT

Four new genera of the family Proedischiidae Pinto & Ornellas, 1978 are described from the Upper Carboniferous of the Bajo de Véliz locality (Argentina): *Velizphlebia cruzi* gen. et sp. n., *Paganzophlebia polyclada* gen. et sp. n., *Irajanarkemina* gen. n. (type species *Narkemina rodendorfi* Pinto & Ornellas, 1978), *Argentinonarkemina* gen. n. (type species *Paranarkemina amosi* Pinto, 1992). The position of the genus *Proedischia* Pinto & Ornellas, 1978 from the Upper Carboniferous, Paraná Basin, is discussed, and Narkeminidae Pinto & Ornellas, 1991 is synonymised with Proedischiidae. Taiophlebiidae fam. n. is described from the Upper Carboniferous of Brazil. New combinations are proposed: *Carpenteroptera rochacamposi* (Pinto & Ornellas, 1978), comb. n., is transferred from the genus *Narkemina* Martynov, 1930 to the genus *Carpenteroptera* Pinto, 1990 (family Carpenteropteridae); *Taiophlebia ferreirai* (Pinto, 1994), comb. n., from the genus *Archaemegaptilus* Pinto, 1994 to the genus *Taiophlebia* gen. n. (family Taiophlebiidae); and *Carpenteroptera rochacamposi* (Pinto & Ornellas, 1978), comb. n., from the genus *Narkemina* to the genus *Carpenteroptera* Pinto, 1990 (family Carpenteropteridae).

KEY WORDS: Insects, Carpenteropteridae, Proedischiidae, Taiophlebiidae, Carboniferous, South America, Argentina, Bajo de Véliz, Brazil, Paganzo Basin, new taxa, new synonymy, new combinations.

INTRODUCTION

As shown in the compilation by Pinto and Adami-Rodrigues (1999) and additions by Pinto *et al.* (2000), Pinto and Sedor (2000), Pinto and Adami-Rodrigues (pers. comm., 2005), the South American Palaeozoic entomofauna is largely diverse, including a rather great number of previously described taxa. But only a few of them are documented by more than a single specimen. This means that more specific field investigations and prospecting work might supply us with a still more diverse insect fauna. In particular, specific Konservat-Lagerstätten for Palaeozoic insects, like those known for younger strata (e.g. the Early Cretaceous Santana area in north-eastern Brazil), are still needed in South America.

The relevant localities are concentrated in southern South America (Paraná Basin of southern Brazil and Uruguay; Paganzo Basin and Central Patagonian Basin in Argentina; Islas Malvinas). One of the localities within the Paganzo Basin—Cuestita de la Herradura near Malazán, La Rioja Province—belongs to the stratigraphically oldest hitherto-known insect-bearing localities (Brauckmann *et al.* 1996).

The present contribution is the first part of a planned series dealing with a detailed systematic review of South American Palaeozoic insects, and is focused on the Ischnoneuroidea–Cacurgoidea complex.

This complex is often controversially discussed in the literature. Martynov (1930) distinguished seven groups within the former "Paraplecoptera", among them the Cacurgoidea which included the families Cacurgidae, Narkemidae and Omaliidae. Sharov (*apud* Storozhenko 1997*b*) proposed the subdivision of the order Paraplecoptera into six superfamilies, among them the Cacurgoidea, including the same three families as in Martynov. Rasnitsyn (*apud* Storozhenko 1997*b*), however, included the Narkemidae within the Grylloblattida Walker, 1914, whereas Storozhenko (1997*b*) considered the Narkemidae as insects *incertae sedis* and also included the Narkeminidae in Grylloblattida.

Rasnitsyn (2002) considered the Narkeminidae, together with the Aetophlebiidae Handlirsch, 1906, as junior synonyms of the Ischnoneuridae Handlirsch, 1906, and attributed them together with the Spanioderidae, Cacurgidae and *Eoblatta* to the eoblattid–spanioderid–cacurgid–narkeminid assemblage of the order Eoblattida.

The adopted terminology of the venation follows Kukalová-Peck (1991).

GEOGRAPHICAL POSITION AND GEOLOGICAL SETTING

Velizphlebia cruzi gen. et sp. n. and *Paganzophlebia polyclada* gen. et sp. n. come from the Bajo de Véliz Formation (Paganzo Basin), San Luis Province (Argentina). This formation crops out at the Bajo de Véliz locality (Fig. 1), which is situated at the north-eastern section of the Sierra Grande de San Luis (32º15'S:65º31'W), about 25 km west of the village of Santa Rosa. Geologically, the Bajo de Véliz Formation (Flores 1969) unconformably overlies the metamorphic basement (composed by greenish phyllites and micaschistes); its thickness is about 164 m. From the bottom to the top three members can be distinguished: (a) Cautana Member (102 m), composed of a basal polymictic conglomerate, thick beds of greenish siltstones with concretions, fine compact greenish-grey sandstone with ondulites and finally a potent series of thick beds of massive arkosic sandstones (light grey and yellow) with thin intercalations of green and delicately stratified siltstones; (b) Pallero Member (53 m), mainly composed of a greyish to greenish shaly siltstone, laminated and with interbedded sandstones, and light greenish, greyish to dark laminated siltstones with beds of dark grey clayey shaly slates, interbedded by fine grained hard sandstones, sometimes calcareous (10–20 cm); (c) Lomas Member (9 m), represented by yellowish to light greenish-brown sandstone of medium to coarse grains in compact beds (0.5–1 m) with crossbedding stratification (Fig. 1B; Hünicken & Pensa 1975; Pinto & Ornellas 1978).

The Pallero Member is uniquely rich in fossils. The fossils include plant macrofossils, palynomorphs, seeds, stems, insects and arachnids. Since the 19th century (Kurtz 1895), different authors have described the geological and palaeontological aspects of this formation in many papers. Compilations were published by Hünicken and Pensa (1975), Hünicken *et al.* (1981), Archangelsky *et al.* (1995,1996), and Azcuy *et al.* (1987).

The Bajo de Véliz Formation has been dated ranging from late Upper Carboniferous to early Lower Permian, up to Upper Permian. The Late Carboniferous age was based on the insect and arachnid assemblage proposed by Pinto and Ornellas (1978, 1980) and Pinto and Hünicken (1980). Azcuy and Jelín (1980) also suggested its probable

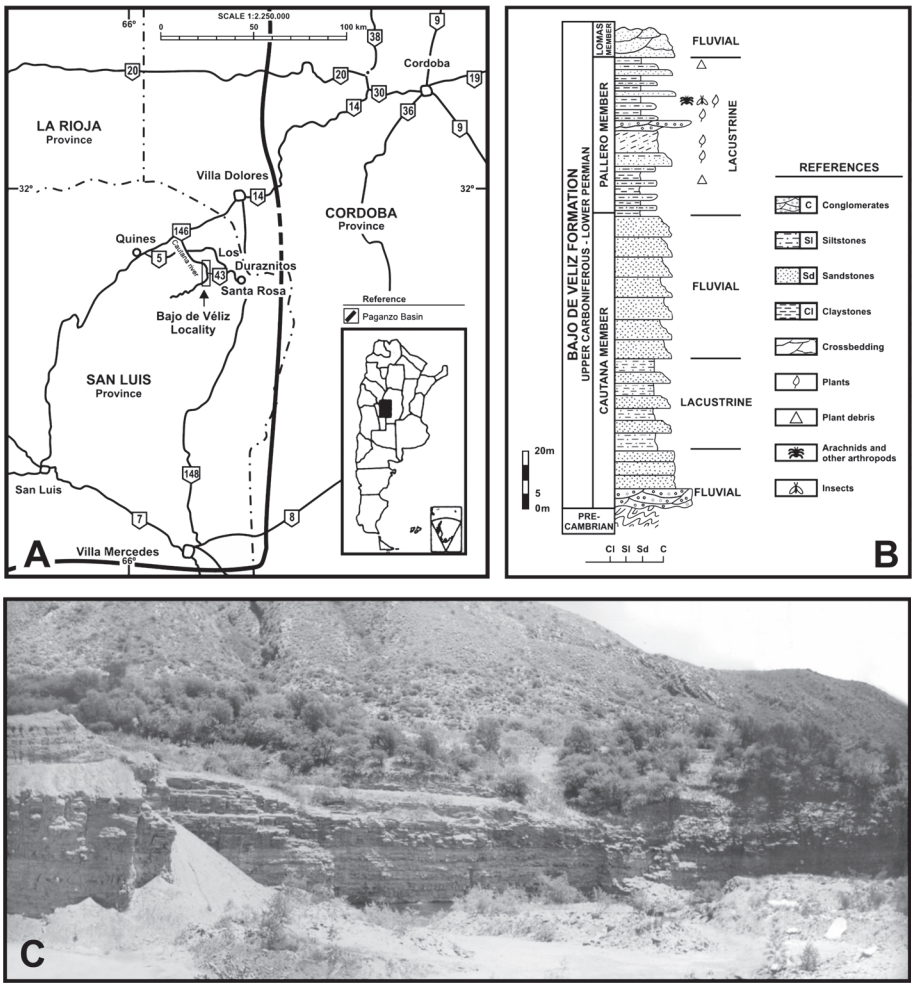


Fig. 1. Bajo de Véliz locality, San Luis province, Argentina: (A) Location map; (B) Stratigraphic section (both adapted from Hünicken & Pensa 1975; Pinto & Ornellas 1978; Azcuy *et al*. 1987); (C) Partial view of a quarry of the outcrop.

Late Carboniferous age (late Stephanian) based on the palynoflora. The fossil plants include species of the *Gangamopteris* biozone and their content corresponds to the Lubeckense flora (Archangelsky & Cúneo 1984; Archangelsky *et al.* 1995, 1996) that corresponds to the Carboniferous–Permian boundary. The palynoflora suggested different age such as Permian (Sakmarian; Menéndez 1971) or earliest Permian (Gutiérrez & Césari 2000). Radiometric dating of other correlated units (e.g. La Colina, La Rioja Province) brings a middle Stephanian age (295 ± 6 Ma, Late Carboniferous; Archangelsky *et al.* 1995). The age of the basement of the Sierra Grande de San Luis is established between 330 and 300 Ma, i.e. Early to Late Carboniferous. Finally the consensus considered the age of the Bajo de Véliz Formation ranging from the latest Carboniferous to the earliest Permian (Gutiérrez 2006).

TAXONOMY

Cohort Polyneoptera *sensu* Gorochov 2001
(= Gryllones *sensu* Rasnitsyn 2002; = Panorthoptera *sensu* Béthoux & Nel 2002)
Order Grylloblattida Walker, 1914 (= Eoblattida *sensu* Rasnitsyn 2002, *partim*)

Superfamily Ischnoneuroidea Handlirsch, 1906, **stat. n.**

Diagnosis: Fore wing with ScP distally fused with RA. CuA short, distally fused with the basal part of MP+CuA.

Constituent families: Ischnoneuridae Handlirsch, 1906; Proedischiidae Pinto & Ornellas, 1978; Taiophlebiidae fam. n.; Spanioderidae Handlirsch, 1906.

Family Proedischiidae Pinto & Ornellas, 1978

Proedischiidae: Pinto & Ornellas 1978: 309 (type genus *Proedischia* Pinto & Ornellas, 1978).
Narkemocacurgidae: Pinto & Ornellas 1978: 310 (not based on valid genus name); 1981: 108.
Narkeminidae: Pinto & Ornellas 1991: 93 (type genus *Narkemina* Martynov, 1930); Storozhenko 1996: 18; 1997*b*: 4; 1998: 69. **Syn. n.**
Narkemidae: Handlirsch 1911: 322 (part.); Martynov 1930: 1229 (part.); Storozhenko 1997*a*: 63 (part.).
Ischnoneuridae: Rasnitsyn 2002: 258 (part.).

Diagnosis: Fore wing with the presence of r–m in the distal part of MA. MP+CuA sigmoid, convergent to MA.

Constituent genera: *Narkemina* Martynov, 1930 (Upper Carboniferous, Kuznetzk Basin, Russia), *Narkeminopsis* Whalley, 1979 (Upper Carboniferous of Great Britain), *Irajanarkemina* gen. n. (Upper Carboniferous, Paraná Basin, Brazil), *Paranarkemina* Pinto & Ornellas, 1980 (Upper Carboniferous, Argentina and Brazil), *Velizphlebia* gen. n. (Upper Carboniferous, Argentina), *Argentinonarkemina* gen. n. (Upper Carbo-niferous, Argentina), *Proedischia* Pinto & Ornellas, 1978 (Upper Carboniferous, Brazil), and *Paganzophlebia* gen. n. (Upper Carboniferous, Argentina). According to Rasnitsyn (pers. comm.), judging from Béthoux and Nel (2005), *Bouleites* Lameere, 1917 could also belong to Narkeminidae (however not examined).

Remarks: Pinto and Ornellas (1978) proposed the family name Narkemocacurgidae for *Narkemina* Martynov, 1930 and related genera to highlight the transitional characters. But since this was not in accordance with the *International Code of Zoological Nomenclature* (ICZN 1985), the same authors (Pinto & Ornellas 1991) replaced this name with Narkeminidae. This was overlooked by Storozhenko (1996), when he also changed the family name into Narkeminidae. As noted below, however, the correct family name for the taxon as defined in this paper is Proedischiidae Pinto & Ornellas, 1978.

The Proedischiidae share a very striking common character in the fore wing: MP+CuA convergent to MA (in some included taxa within the family, this vein is strongly convergent). This feature is not present within the *Ischnoneura–Spaniodera–Cacurgus–Eoblatta* complex, and therefore we do not regard the Proedischiidae and Ischnoneuridae as synonymous as Rasnitsyn (2002) did. Rasnitsyn (pers. comm.), after examining the type genus, considers Aetophlebiidae Handlirsch, 1906 as fitting the diagnosis of Proedischiidae perfectly (cf. original description of *Aetophlebia singularis* by Scudder, 1885, fig. 9). If so, it could be concluded that Proedischiidae is a junior synonym of Aetophlebiidae, the older name. However, the type genus as figured by Handlirsch

(1906–08, pl. XVI, fig. 14) neither has ScP distally fused nor the typical short CuA distally fused with MP+CuA, as proposed here for the Proedischiidae, so excluding it from the Proedischiidae.

Genus **Irajanarkemina** Martins-Neto, Gallego & Brauckmann, gen. n.

Etymology: In honour of Prof. Dr Irajá Damiani Pinto (UFRGS, Brazil), the first and outstanding scientific investigator of the South American Palaeozoic entomofauna, and *Narkemina*, the closely related genus. Gender feminine.

Type species: *Narkemina rodendorfi* Pinto & Ornellas, 1978, designated here.

Diagnosis: Fore wing relatively wide. ScP distally fused with RA. Origin of RP close to apex of wing, far from origin of MP. MP+CuA strongly convergent to MA with the secondary branches notably curved toward the anal margin. Supporting cross veins r–m and ma–mp present. Origin of CuP not directly from the distal part of CuA.

Discussion: *Irajanarkemina* gen. n. differs from *Narkemina*, the closest genus, by having a wider fore wing (relatively narrow in the hitherto known species of *Narkemina*), MP+CuA less strongly convergent to MA, the secondary branches of which are notably curved toward the anal margin (Fig. 2) (straight and oblique to the anal margin in *Narkemina*).

Species included: Type species only.

Irajanarkemina rodendorfi (Pinto & Ornellas, 1978), **comb. n.**

Fig. 2

Narkemina rodendorfi: Pinto & Ornellas 1978: 311, pl. I, figs 4, 5; pl. II, figs 2, 3 (holotype MP-I-5283a, b; São Paulo, Upper Carboniferous; in UFRGS, Brazil; studied); Storozhenko 1998: 71, fig. 114.
Narkemina rohdendorfi: Pinto 1995: 47 (unjustified emendation); Pinto & Adami-Rodrigues 1999: 122 (unjustified emendation).

Remarks: In the original description, Pinto and Ornellas (1978) considered the holotype specimen as a hind wing. The absence of a typical anal fan as known from typical hind wings of other species of the Proedischiidae leads us to regard it more likely as a fore wing, however.

Pinto and Ornellas (1978) originally spelled the specific name "*rodendorfi*" which is possible if it is derived directly from the Russian (Cyrillic) spelling. Later the authors changed it to "*rohdendorfi*", the spelling which B.B. Rohdendorf himself preferred to use in transliterations of his name. According to Article 32.5.1 of the *International*

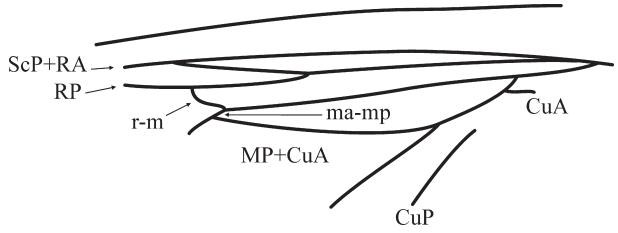
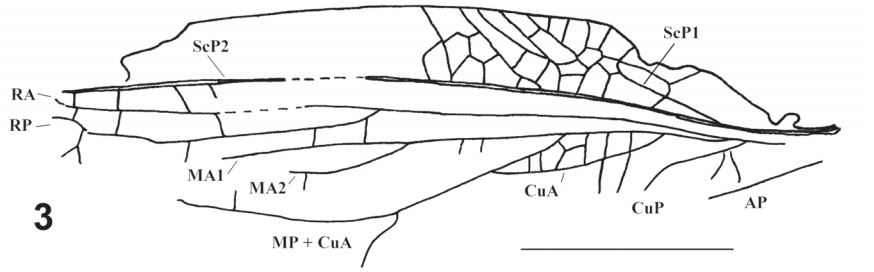
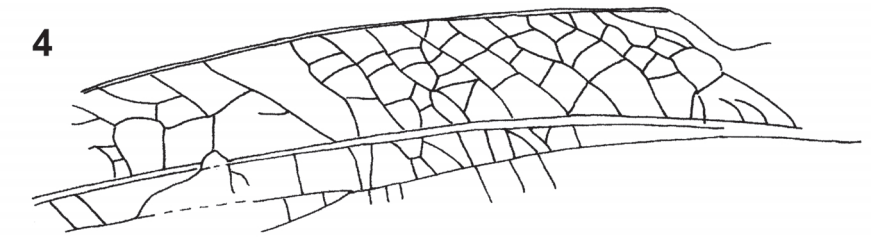
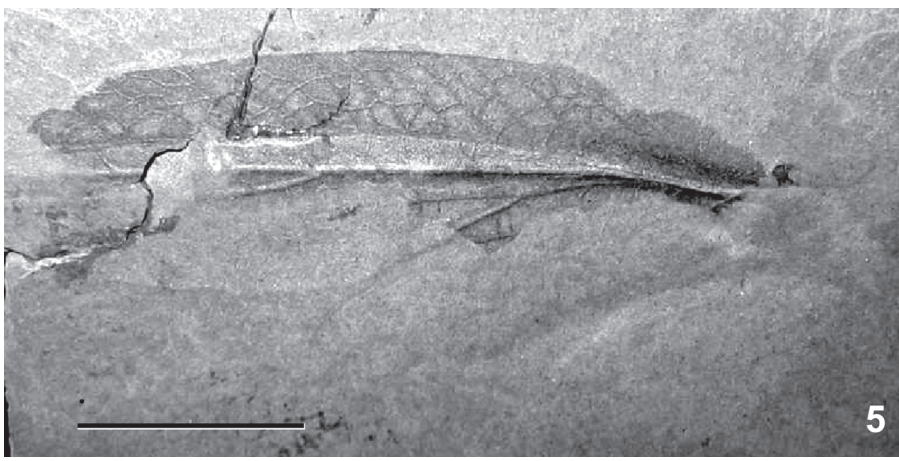


Fig. 2. *Irajanarkemina rodendorfi*, main venational pattern, schematic drawing. CuA, CuP, anterior and posterior cubitus; MA, MP, anterior and posterior media; RA, RP, anterior and posterior radius; ScA, ScP, anterior and posterior subcosta; r–m, supporting cross vein radius–media; ma–mp, supporting cross vein anterior–posterior media.







Figs 3–5. *Velizphlebia cruzi* gen. et sp. n., holotype, MHIN-UNSL-GEO-I 484: (3) wing venation; (4) details of costal area; (5) general appearance of specimen. Vein designations: see Fig. 2. Scale bars = 10 mm.

Code of Zoological Nomenclature (ICZN 1999), incorrect transliteration is not an inadvertent error and therefore does not require correction.

Genus **Velizphlebia** Martins-Neto, Gallego & Brauckmann, gen. n.

Etymology: After the Bajo de Véliz locality, Argentina, and *phlebia* = vein (latinized form of Greek *phleps*). Gender feminine.

Type species: *Velizphlebia cruz*i sp. n., designated here.

Diagnosis: Forewing relatively wide. Very wide and reticulate costal space and very basal MA fork. ScP distally fused with RA. Origin of RP at mid-length of the wing and

far from origin of MP. MP+CuA strongly convergent to MA. Origin of CuP not directly from distal part of CuA.

Discussion. Similar to *Narkemina* and *Irajanarkemina* in having ScP distally fused with RA and MP+CuA strongly convergent to MA; differing however in having the origin of RP relatively far from the wing apex (although also far from the origin of MP) and the origin of CuP not directly from the distal part of CuA. Additionally the very wide and reticulate costal space and very basal MA fork are features completely different from the rest of the Proedischiidae.

Velizphlebia cruzi Martins-Neto, Gallego & Brauckmann, sp. n.

Figs 3–5

Etymology: In honour of Lic. Jorge Cruz (Mendoza, Argentina) who collected the specimen.

Description: Preserved length, 50 mm. Costal area relatively wide and filled with anastomosed cross-veins (Fig. 4). ScP1 conspicuous at the wing base and ScP distally fused with RA which is slightly curved. Origin of RP near mid-length of wing, apparently unbranched. MA two-branched. MP+CuA strongly convergent to MA. CuA short, distally fused with MP. CuP not directly branching from distal part of CuA.

Holotype: MHIN-UNSL-GEO-I 484, Museo de Historia Natural de la Universidad Nacional de San Luis, Geología; fragment of fore wing. ARGENTINA: Bajo de Véliz locality; Upper Carboniferous to Lower Permian, Pallero Member, Bajo de Véliz Formation.

Genus *Paranarkemina* Pinto & Ornellas, 1980

Paranarkemina: Pinto & Ornellas 1980: 288.

Type species: *Paranarkemina kurtzi* Pinto & Ornellas, 1980, by original designation.

Emended diagnosis: Fore wing relatively wide. ScP distally fused with RA. Origin of RP close to the origin of MP. MP+CuA not strongly convergent to MA. Supporting cross vein ma–mp absent. CuP convergent and distally fused with AP.

Comparison: *Paranarkemina* differs from the other known genera of the Proedischiidae, except *Argentinonarkemina* gen. n., in having the origin of RP close to the origin of MP. See schematic pattern of the main veins in Fig. 6.

Constituent species: *P. kurtzi* Pinto & Ornellas, 1980 (= *P. velizensis* Pinto & Ornellas, 1981) (Upper Carboniferous, Argentina) and *P. martinsnetoi* Würdig, Pinto & Adami-Rodrigues, 1998 (Upper Carboniferous, Paraná Basin, Brazil).

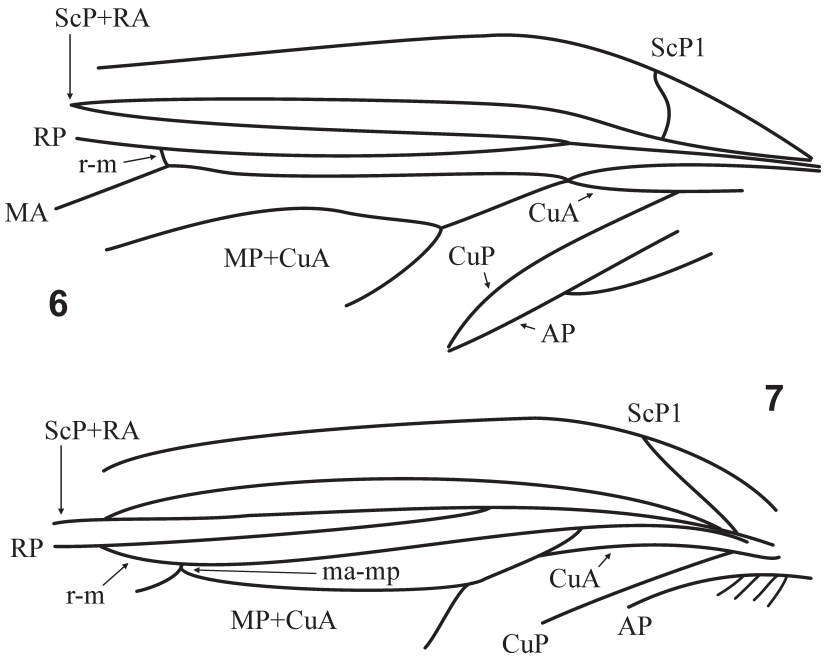
Remarks: Storozhenko (1998) considered *Paranarkemina velizensis* as a fragment of the hind wing of the last-instar subimago of *P. kurtzi* and synonymised both species, with which we agree.

Genus **Argentinonarkemina** Martins-Neto, Gallego & Brauckmann, gen. n.

Fig. 7

Etymology: After Argentina, where the material comes from, in combination with *Narkemina*. Gender feminine.

Type species: *Paranarkemina amosi* Pinto, 1992, here designated.



Figs 6, 7. Schematic drawing of wing venation: (6) *Paranarkemina martinsnetoi*; (7) *Argentinonarkemina amosi*. Vein designations: see Fig. 2.

Diagnosis: Origin of RP close to origin of MP. MP+CuA strongly convergent to MA, ma–mp present and CuP not distally fused with AP.

Comparison: Similar to *Paranarkemina* in having the origin of RP close to the origin of MP, differing however by having MP+CuA strongly convergent to MA, and ma–mp present, as well as CuP not distally fused with AP.

Species included: *Argentinonarkemina amosi* (Pinto, 1992), **comb. n.**

Genus *Proedischia* Pinto & Ornellas, 1978

Proedischia: Pinto & Ornellas 1978: 309.

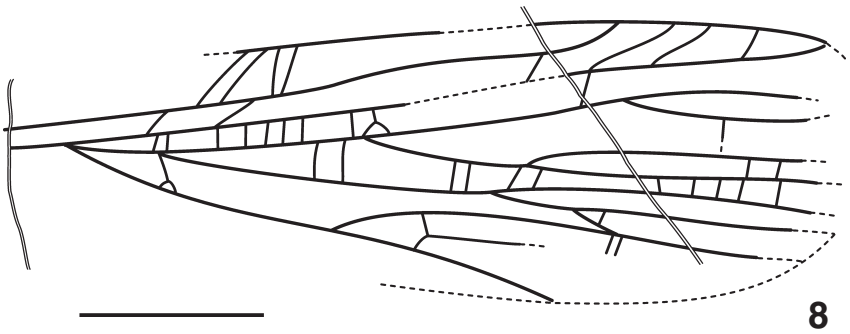
Type species: *Proedischia mezzalirai* Pinto & Ornellas, 1978, by original designation.

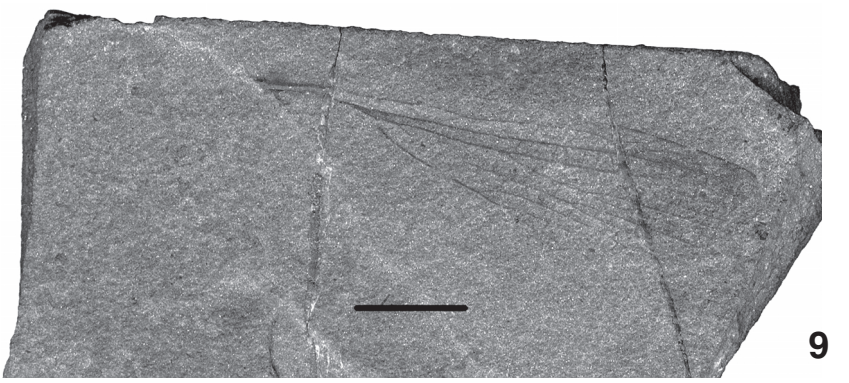
Emended diagnosis: Hind wing long and relatively narrow. ScP not distally fused with RA, but RA distally fused with RP. Origin of RP at mid-length of wing. Supporting cross vein r–m present, forming a conspicuous jugum-like constriction between RP and MA.

Comparison: *Proedischia* differs from *Narkemina* by having ScP not distally fused with RA and the origin of RP far from the wing base (very close to the wing base in *Narkemina* species).

Species included: Type species only.

Remarks: Pinto and Ornellas (1978) originally described this wing as a forewing belonging to the "Protorthoptera", and established a separate family Proedischiidae. But there are striking similarities with the Narkeminidae, as for example the long and





Figs 8, 9. *Paganzophlebia polyclada* gen. et sp. n., holotype, MHIN-UNSL-GEO-I 485: (8) details of venation; (9) general appearance of specimen. Scale bar = 10 mm.

oblique CuA. The main differences between *Proedischia* and *Narkemina* are restricted to the lack of a distal fusion of ScP and RA in *Proedischia*. This character removes it from *Narkemina* (with the best-known hind wings). Judging only from the position and course of RP, *Proedischia mezzalirai* could be attributed to the genus *Velizphlebia*. But in the hitherto-known species the position and course of these veins are different in the fore and hind wings. Therefore we prefer to maintain *Proedischia* as a separate genus until more complete material is available, but regard the family Proedischiidae as synonymous with the Narkeminidae. If so, the name Proedischiidae established in 1978 has priority.

Genus **Paganzophlebia** Martins-Neto, Gallego & Brauckmann, gen. n.

Etymology: After the Paganzo Basin, Argentina, where the material comes from, and *phlebia* = vein (latinized form of Greek *phleps*). Gender feminine.

Type species: *Paganzophlebia polyclada* sp. n., here designated.

Diagnosis: ScP distally sigmoid, not fused distally with RA. RP originating at wing mid-length. RA and RP distally branched, not fusing.

Comparison: Similar to *Proedischia* in having the hind wing with ScP not fused distally with RA and the origin of RP at the mid-length of the wing, but markedly differing in the distally sigmoidal ScP and distally branched and not fusing RA and RP.

Species included: Type species only.

Remarks: The specimen presents another hind wing of strong narkeminid affinities which cannot be exactly placed into a described genus. In several aspects the new taxon closely resembles the hind wings of the species of *Narkemina*, except for the absence of the distal fusion of ScP and RA. In this character, *Paganzophlebia* is similar to *Proedischia*, but it clearly differs from the latter in the much more slender shape which is more similar to typical members of the Proedischiidae. This is why we prefer to establish a separate genus. Future additional material should show if it could be maintained.

Paganzophlebia polyclada Martins-Neto, Gallego & Brauckmann, sp. n.

Figs 8, 9

Etymology: From Greek *poly* (many) and *clados* (branch), after the rich venation of the holotype specimen; here used as an adjective.

Description: Preserved length, 53 mm. ScP slightly sigmoidal, not distally fused with RA. RP two-branched, each branch distally dichotomising. Origin of RP very close to the wing base. MA simple, MP two-branched, with MP2 short, distally fused with CuA1. CuA long, slightly curved: CuA1 long and parallel to MP2; CuA2 shorter than CuA1, oblique to the anal margin.

Holotype: MHIN-UNSL-GEO-I 485, Museo de Historia Natural de la Universidad Nacional de San Luis, Geología; hindwing fragment, CuP not preserved. ARGENTINA: Bajo de Véliz locality; Upper Carboniferous to Lower Permian, Pallero Member, Bajo de Véliz Formation.

Family **Taiophlebiidae** Martins-Neto, fam. n.

Type genus: *Taiophlebia* Martins-Neto, gen. n.

Diagnosis: Fore wing with ScP and RA distally fused and RP multi-branched. RP origin at 1/5 of the wing base.

Genus **Taiophlebia** Martins-Neto, gen. n.

Taiophlebia: Martins-Neto *et al.*, 2004: 45.

Etymology: From the type locality and *phlebia* = vein (latinized form of Greek *phleps*). Gender feminine.

Type species: *T. niloriclasodae* Martins-Neto, sp. n., by present designation.

Diagnosis: Fore wing with more than 100 mm long. Costal margin straight. Sc branching in ScA and ScP. ScP with at least two strong secondary branches. ScP/RA fused circa 1/4 of the wing apex. CuA most proximal branch reaches the anal margin after the wing midlength.

Species included: The type species and *Taiophlebia ferreirai* (Pinto, 1994), comb. n.

Remarks: *T. niloriclasodae* from the upper part of the Rio do Sul Formation at the Taió municipality, Santa Catarina, Brazil (Upper Carboniferous, Paraná Basin) is a key taxon for the understanding of the Ischnoneuroidea–Cacurgoidea complex. Particular characters of the venation such as the distal fusion of ScP and RA, and RP originating close to the basal fifth of the wing support a closer relationship to the representatives of the Ischnoneuroidea (Grylloblattida *sensu* Storozhenko), rather than to the Cacurgoidea

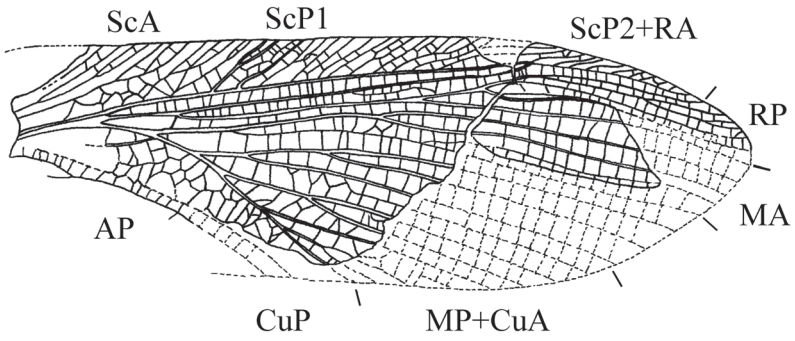


Fig. 10. *Taiophlebia niloriclasodae*, reconstructed forewing (after Dutra *et al*. in press). Vein designations: see Fig. 2.

("Paraplecoptera" *s.l.* or Orthoptera). The Taiophlebiidae differ from the Proedischiidae as well as from their closest related families by the lack of the typical convergence of MP+CuA and thus represent the most basal group within the Ischnoneuroidea–Cacurgoidea complex. Another genus, *Cacurgulopsis* Pinto & Adami-Rodrigues, 1995 from Boituva, São Paulo (Paraná Basin, Upper Carboniferous) was originally included in the family Cacurgidae. However, in *Cacurgus* Handlirsch, 1911, the type genus of this family, ScP is not distally fused with the multibranched RA, originating in the basal third of the wing. *Cacurgulopsis* and *Taiophlebia* seem to be sister genera and are therefore included in the family Taiophlebiidae (Dutra *et al.* in press).

Taiophlebia niloriclasodae Martins-Neto, sp. n.

Fig. 10

Etymology: Anagram derived from Nilson, Lorelai, Rita, Claus, Sonis, and Daiana, dynamic students of Geosciences Department, Universidade do Vale do Rio dos Sinos–UNISINOS, leadered by Dr Tania Lindner Dutra, the team that collected the holotype.

Description: Fore wing 104 mm long and 34 mm wide, as preserved, with straight costal margin and slightly acuminate apex. Subcostal area notably wide close the base, progressively narrowing toward the apex. ScA well-defined with numerous secondary veinlets and anastomosed pattern of cross-veins. ScP long with at least two strong secondary branches and several, relatively long, distally dichotomous veinlets, unbranched. RP origin at 1/5 of wing base. RP slightly sigmoid, with five secondary branches. MA long, slightly sigmoid, three-branched. MP+CuA origin little before RP origin level with at least eight terminal branches, clade-like. CuP two-branched with CuP1 being the smallest, converging to MP+CuA, fusing distally; CuP partially preserved, oblique to anal margin, reaching it at about 1/3 of wing base. AP1 fuses to AP2 close to the wing base, Y-shaped. AP1+2 parallel to CuP2. Intense pattern of cross-veins forming mosaics of heterogeneous cells in the whole preserved wing. No ornamentation pattern.

Holotype: BRAZIL: *Santa Catarina State*: Taió municipality; Upper Carboniferous, Itararé Subgroup, upper part of the Rio do Sul Formation. Housed at Geosciences Department, UNISINOS, Rio Grande do Sul, Brazil.

Taiophlebia ferreirai (Pinto, 1994), **comb. n.**

Archaemegaptilus ferreirai Pinto, 1994: 107–108, fig. 1 (holotype BA-PB-638, studied).

Remarks: *A. ferreirai* from the Upper Carboniferous (Piedra Shotle Formation, Chubut) of Argentina, was originally attributed to the palaeodictyopterans but clearly exhibits characters typical for *Taiophlebia*, and can be therefore transferred to the latter genus.

Superfamily Cacurgoidea Handlirsch, 1911

Several Carboniferous families were established on very fragmentary material and therefore their exact systematic positions and affinities are far from clear. The family Cacurgidae Handlirsch, 1911 was originally proposed for *Cacurgus* Handlirsch, 1911 from the Pennsylvanian of Mazon Creek, Illinois (USA). Carpenter (1943) as well as Brauckmann and Koch (1982) included *Heterologus* Carpenter, 1944 from Mazon Creek and *Heterologopsis* Brauckmann & Koch, 1982 from the Upper Namurian of Germany in this family. *Cacurgulopsis* Pinto & Adami-Rodrigues, 1995 from the Boituva locality (Paraná Basin, Upper Carboniferous of Brazil, discussed above) was additionally included by Pinto and Adami-Rodrigues (1995). However, *Cacurgus*, the type genus of the family, has ScP not distally fused with RA, a multibranched RA, origin of RP about 1/3 distally from the wing base, and therefore shows characters which are completely distinct from *Heterologus*, *Heterologopsis, Cacurgulopsis* and *Taiophlebia*, all of them with ScP and RA distally fused, unbranched RA, multibranched RP and origin of RP about 1/5 from wing base. Other families (Ampelipteridae Haupt, 1940 for *Ampeliptera* Pruvost, 1927, from the Upper Namurian of The Netherlands; Omaliidae Handlirsch, 1906 for *Omalia* van Beneden & Coemans, 1867 from the Westphalian of Belgium; and Carpenteropteridae Pinto & Ornellas, 1991 for *Carpenteroptera* Pinto, 1990) have the origin of RP 1/3 to 1/2 the distance from the wing base.

Family Carpenteropteridae Pinto & Ornellas, 1991

Cacurgonarkemidae: Pinto 1990: 7 (not based on valid genus name).
Carpenteropteridae: Pinto & Ornellas 1991: 93.

Diagnosis: See Pinto (1990: 7).

Carpenteroptera Pinto, 1990

Carpenteroptera: Pinto 1990: 7.

Type species: *Carpenteroptera onzii* Pinto, 1990, by original designation.

Diagnosis: See Pinto (1990: 7).

Species included: *C. onzii* Pinto, 1990 and *C. rochacamposi* (Pinto & Ornellas, 1978), comb. n.

Carpenteroptera rochacamposi (Pinto & Ornellas, 1978), **comb. n.**

Narkemina rochacamposi: Pinto & Ornellas 1978: 312, pl. II, figs 4a, b (holotype MP-I-5286; Rio Grande do Sul, Upper Carboniferous; in UFRGS; studied); Storozhenko 1998: 72.

Remarks: When describing *C. onzi*, Pinto (1990) pointed out the similarity of this species to the previously described *N. rochacamposi* Pinto and Ornellas, 1978. Judging from the published drawings, *N. rochacamposi* and *C. onzi* belong to the same genus,

Carpenteroptera, and, after new knowledge (in particular on intraspecific variation) from the whole complex, maybe to the same species. But this decision cannot be made at this stage, because *C. rochacamposi* was based on a very fragmentary specimen, and it is impossible to compare it in detail with the more completely preserved *C. onzi*.

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Lower Jurassic cockroaches (Insecta: Blattaria) from Germany and England

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ABSTRACT

Types of the Lower Jurassic cockroaches described by Geinitz, Scudder, Handlirsch and Bode from Germany and England are redescribed. Forty-five previously described Lower Toarcian cockroach species are synonymised into six species. The type genera of the Mesoblattinidae (*Mesoblattina* Geinitz, 1880) and Caloblattinidae (*Caloblattina* Handlirsch, 1906) with their type species *Blattina protypa* Geinitz, 1880 and *Blattina mathildae* Geinitz, 1883 are restudied. Redescribed are the holotypes of the Lower Liassic *Mesoblattina geikiei* Scudder, 1886 and the Lower Toarcian *Mesoblattina blakei* Scudder, 1886. The systematic affinity of *Eublattula crassivena* Handlirsch, 1939 is still unresolved. The variability of the 88 studied specimens of the dominant Lower Toarcian cockroach *Blattula langfeldti* (Geinitz, 1880) (Blattulidae) is found to be much greater than the variability of Lower Cretaceous Blattulidae of the same size. Compared with most sites of the Middle–Late Jurassic and Early Cretaceous world-wide, the diversity of the studied Lower Jurassic cockroaches is surprisingly low, probably as a result of destabilised ecosystems of the island source areas.

KEY WORDS: Blattaria, Blattidae, Blattulidae, Caloblattinidae, Mesoblattinidae, cockroaches, Jurassic, Toarcian, England, Germany, revision, new synonymy.

INTRODUCTION

Cockroaches are among the most abundant terrestrial arthropods in the non-marine Late Palaeozoic–Mesozoic fossil record. Thus, in the case of their detailed study they may represent fine evolutionary, not to mention stratigraphical, data. Nevertheless, knowledge of their role in the ecosystems of the past is still scarce.

The present work gives evidence of the necessity for redescription of the earlier-studied type material, after which the extensive cockroach diversity of some Triassic and Early Jurassic sites appears very limited. The cockroach diversity of the European Early Toarcian sites is found to be low, even when compared to most of the Jurassic sites. Nevertheless, the abundance of the most common species reveals useful data on the variability of the wing venation, which highlight some specific aspects of the group in general, such as changes in control mechanisms, variability changes (ecological plasticity of species), etc. (Vršanský 2000). The most fascinating result of the above-mentioned study was, in particular, the decreasing variability of species from the Carboniferous to the present, supported by results of the present study.

The Early Jurassic is rather static with regards to the evolution of the cockroach fauna. Palaeozoic Phyloblattidae and Archimylacrididae as well as Mesozoic groups are present during this time. In the German localities of the Early Toarcian, Mesoblattinidae, Blattulidae, Caloblattinidae and a new family (to be established for *Rhipidoblattina* and related genera on the basis of better and more complete material (Vršanský, in press)) are present in low diversity (five species of 119 studied specimens).

The systematic position of *Eublattula crassivena* Handlirsch, 1939 remains disputable. The material described below is of particular importance, since it comprises the types of Geinitz (1880, 1883, 1884, 1887), Scudder (1886), Handlirsch (1906–08, 1920, 1939) and Bode (1953), including the types of an abundant Mesozoic cockroach family, Caloblattinidae, and Mesoblattinidae. The type of *Mesoblattina protypa* evidently differs from other species placed into Mesoblattinidae in the past. All the known species, except for the type and some additional species, were removed and placed within Caloblattinidae (Vršanský 2000) and in a new family (Vršanský, in press). A number of "mesoblattinids" were previously removed from the Mesoblattinidae to Blattulidae (Vishniakova 1982). The Mesoblattinidae is now found to be restricted to the Jurassic and Early Cretaceous, representing a progressive evolutionary stem, ancestral to modern Blattidae, Blattellidae (Vršanský *et al.* 2002; Vršanský 2002) and probably also Blaberidae. The Mesoblattinidae most probably evolved from the new family, to be established for *Rhipidoblattina* and other genera, or its ancestors during the Late Triassic–Early Jurassic. Finally, the current detailed observations of the cockroach fauna of the Early Cretaceous (Vršanský 1999*a*, *b*, 2000, 2002; Vršanský & Ansorge 2001; Vršanský *et al.* 2001, 2002) allow us to compare some aspects of the Jurassic–Cretaceous stages within the evolution of Blattaria.

LOCALITIES AND MATERIAL

A number of very rich Lower Toarcian (Late Liassic, Early Jurassic) insect localities is known in Europe. These localities are situated in Germany, Luxembourg/Belgium and England (Ansorge 1996, 2003, 2004). All Upper Liassic insects in Europe originate from limestone concretions which are intercalated within Posidonia Shale, except for north-eastern Germany where the concretions were formed in plastic clay of the "Green Series". The insects were buried as a component of a marine taphocoenosis; they are associated with marine molluscs such as ammonites, theutoids, bivalves and gastropods. Fishes and reptiles are also present. Besides driftwood and extremely rare terrestrial reptiles, insects appear to be the most numerous of land inhabitants. Associated ammonites indicate the presence of the *falciferum* Zone, subdivided into the lower *elegantulum* Subzone and the subsequent *exaratum* Subzone.

Cockroaches have been described from several Lower Toarcian localities in Europe. The first cockroaches were described by Geinitz (1880, 1883, 1884, 1887) from Dobbertin in Mecklenburg, Germany. At the same time, Scudder (1886) reported two cockroach species from the Lower Toarcian of Gloucestershire in England. Handlirsch (1906–08, 1920, 1939) restudied the types from Germany and England and added a number of new species from Dobbertin. Bode (1953) described a number of Blattaria from several different localities (Hondelage, Schandelah, Hattorf) in the vicinity of Braunschweig (Brunswick, Lower Saxony, Germany). Almost all of these species were based on the holotypes only. Brachert (1987) mentioned the presence of cockroaches in a temporary outcrop at the Rhine-Main-Donau canal near Kerkhofen in Bavaria (Germany). Berger (1989) figured one species from the same locality. Delsate *et al.* (1992) reported two specimens from the Lower Toarcian Posidonia Shale of Belgium.

In recent years the junior author collected some thousands of fossil insects in the Lower Toarcian of Grimmen (Western Pomerania), Dobbertin (Mecklenburg),

Schandelah near Brunswick (Lower Saxony) and Mistelgau near Bayreuth (Bavaria). From his data the following percentages of cockroaches were counted: Grimmen, 2.0% of 2042 insects; Dobbertin, 4.3% of 958 insects; Brunswick, 0.4% of 663 insects; Mistelgau, 1.6% of 176 insects. These percentages are mostly considerably lower than the data from the material studied by Handlirsch (Dobbertin, 7.2%) and Bode (Brunswick, 3.0%). These smaller percentages of cockroaches in the fossil material may be a result of a subjective preference which earlier collectors might have had for larger insects. Cockroaches are also present in the famous Posidonia shales of Holzmaden (*Liadoblattina blakei*) and in the Posidonia shales of Bascharage in Luxembourg (Henrotay *et al.* 1998).

The geographical positions of the mentioned Lower Toarcian localities are as follows: Dobbertin (Mecklenburg) [53°61'50"N:12°11'10"E], Grimmen (Western Pomerania) [54°13'30"N:13°06'00"E], Schandelah (Lower Saxony) [52°28'50"N:10°70'70"E], Mistelgau (Bavaria) [49°28'40"N:11°46'60"E], Kerkhofen (Bavaria) [49°16'20"N:11°39'30"E], Holzmaden (Württemberg) [48°63'50"N:9°52'70"E], Bascharage (Luxembourg) [49°56'20"N:5°91'70"E], Alderton (Gloucestershire) [52°00'N:2°00'W].

About 120 cockroaches, mainly wings, were studied from these localities (Table 1).

The type material is kept in the Institut für Geologische Wissenschaften, der Ernst-Moritz-Arndt Universität Greifswald (FGWG); Roemer-Pelizaeus Museum Hildesheim (Hi); Geologisch-Paläontologisches Institut, TU Clausthal-Zellerfeld (Cl); Geologisch-Paläontologisches Institut der Universität Göttingen (G); Forschungsinstitut Senckenberg, Frankfurt am Main (SNM; W, former Wunnenberg collection; B, former collection of Technische Hochschule Braunschweig); Naturhistorisches Museum, Vienna (NHMW); Natural History Museum, London (NHML). The specimens labelled LGA (Grimmen), LDA (Dobbertin), S (Schandelah), M (Mistelgau) are from the private collection of J. Ansorge, later to be housed at the Museum für Naturkunde der Humboldt Universität, Berlin.

Photographs were taken with a NIKON Coolpix 4500 digital camera, adapted to various optical equipment; drawings are camera-lucida based or re-drawn photographs using ROTRING pens.

Abbreviations used: Fw – forewing; Hw – hindwing; Sc – subcosta; R – radius; RS – radial sector; M – media; CuA – cubitus anterior; CuP – cubitus posterior; A – anal veins.

TABLE 1

Material studied from the German Lower Toarcian localities.

	Dobbertin		Grimmen		Brunswick		Mistelgau		Holzmaden		TOTAL
	Fw	Hw	Fw	Hw	Fw	Hw	Fw	Hw	Fw	Hw	
Blattula langfeldti	32	20	14	18	4	-	-	-	-	-	88
Blattula dubia	-	2	1	-	-	-	-	-	-	-	3
Eublattula crassivena	1	-	-	-	-	-	-	-	-	-	1
Mesoblattina protypa	3	-	2	-	-	-	2	-	-	-	7
Caloblattina mathildae	3	-	-	-	5	2	-	-	-	-	10
Liadoblattina blakei	2	2	-	-	1	3	-		2	-	10
TOTAL	41	24	17	18	10	5	2	0	2	0	119

TAXONOMY

Order Blattaria Latreille, 1810

Superfamily Blattoidea Latreille, 1810

Family Mesoblattinidae Handlirsch, 1906

Type genus: *Mesoblattina* Geinitz, 1880.

Diagnosis: Medium-sized cockroaches, plesiomorphically with short external ovipositor, with generally reduced and regular venation (with exception of area between bases of M and R) without branchlets, and with dense venation present in apical parts of R and M in forewing. Forewings with more or less parallel borders, without distinct intercalaries. A without numerous reticulations; venation of Cu and M, with exception of the first stem, regular; R straight; Sc two- to four-branched. Hindwing with simple Sc; R1 and RS differentiated; M with up to 5 branches; CuA secondarily branched and with additional blind branches; CuP simple.

Composition: *Mesoblattina* Geinitz, 1880; *Hispanoblatta* Martínez-Delclòs, 1993; *Archimesoblatta* Vršanský, 2003; *Praeblattella* Vršanský, 2003; *Breviblattina* Vršanský, 2004; *Mongolblatta* Vršanský, 2004 and a new genus represented by "*Artitocoblatta*" *colominasi* Meunier, 1914.

Remarks: The family represents the most advanced group of Lower Jurassic cockroaches, ancestral to contemporary lineages of Blattidae, Blattellidae and Blaberidae. The latest mesoblattinids share strong synapomorphies with Blattellidae and Blattidae (regular venation; forewing with parallel borders, RS differentiated, simple A; hindwing with simple CuP). Early Blattidae differ only in hindwing M which is branched, and the Mesoblattinidae (*Praeblattella*, *Hispanoblatta,* etc.) in possessing a short, rudimentary external ovipositor (the composition of the terminalia is a diagnostic character for Blattidae and Blattellidae).

The Mesoblattinidae evolved during the earliest Jurassic or possibly earlier (Vršanský 2003) from the stem group including the Caloblattinidae and a new family, or directly from the new family erected for *Rhipidoblattina* and other genera (Vršanský, in press).* They are synapomorphic in the hindwing composition with R comb-like, blind branches of CuA and simple CuP. They also share branched Sc in the forewing, some apical branchlets in A, and irregularity of venation (all plesiomorphies). The irregularity of venation is a strong plesiomorphy. The regularity of venation means that the distance between the competent veins is constant (exceptions might be Sc–R and the clavus with its branches, which have both supportive and/or protective functions). This regularity is affected only by the dichotomy and only immediately after the fork, as if it were stabilised by some tending force. This is not the case in the Palaeozoic Blattaria. In early Mesoblattinidae the regularity of venation may not occur in the apical parts of the wing and in the uppermost branch of M, where irregularity is present even before the M branching (late Caloblattinidae and representatives of a new family have also lost these plesiomorphic irregularities).

* Caloblattinidae are autapomorphic in the wide forewing and modified habitus; the new family is characterised by a shorter ovipositor and is apomorphic in branched A1 attached to the remigial part of the wing.

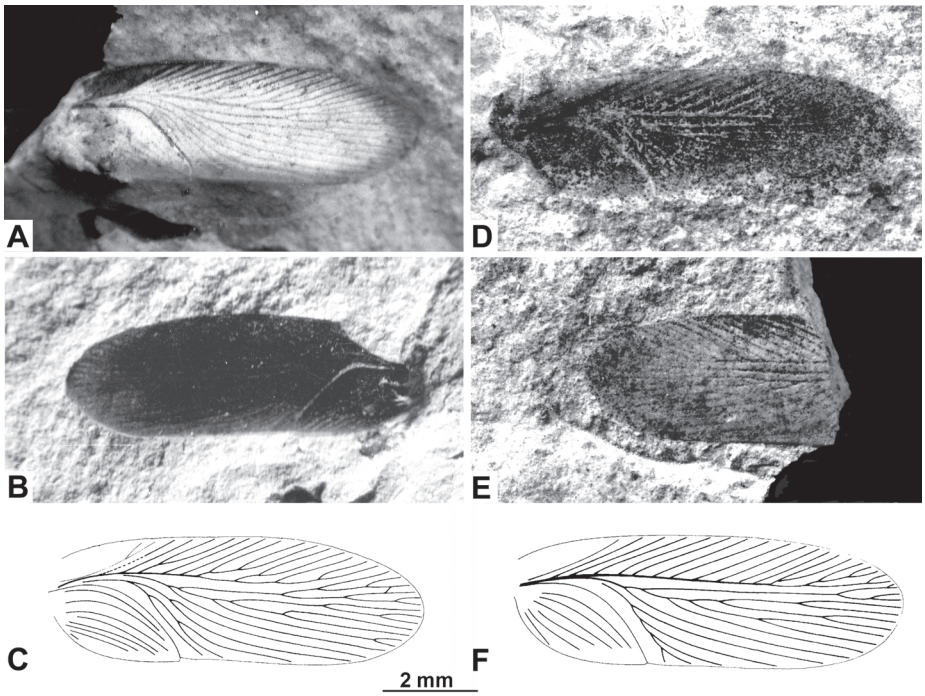

Fig. 1. *Mesoblattina protypa* Geinitz, 1880: (A–C) LGA 1942, forewing, Lower Toarcian of Grimmen; (D–F) FGWG 117/1, holotype, forewing, Lower Toarcian of Dobbertin.

Genus *Mesoblattina* Geinitz, 1880

Mesoblattina: Geinitz 1880: 519.

Type species: *Blattina* (*Mesoblattina*) *protypa* Geinitz, 1880; Lower Toarcian, Dobbertin, Germany.

Diagnosis: Forewings coriaceous, well sclerotised, with strictly parallel borders; Sc simple; R very straight, not distinguished into R and RS, with simple branches (apical branches are the exception); A not branched up to the apical third, clavus very short. Local irregularities of venation present.

Composition: Type species only.

Remarks: Other species previously assigned to *Mesoblattina* do not belong to this genus nor to the family Mesoblattinidae, and should be transferred, in most cases, into Caloblattinidae or into a new family (Vršanský, in press).

The forewing venation generally resembles *Praeblattella* Vršanský, 2003, which differs in having fully regular venation. Most closely related is apparently *Mongolblatta* Vršanský, 2004 from the Tithonian of Shar-Teg in Mongolia (synapomorphic in having coriaceous forewings) which differs in having regular venation and tuberculated anal veins (apomorphies).

With respect to all other representatives of the family Mesoblattinidae, even the oldest known is apomorphic in having coriaceous wing membranes. A phylogenetic system of the Mesoblattinidae has been presented by Vršanský (2003).

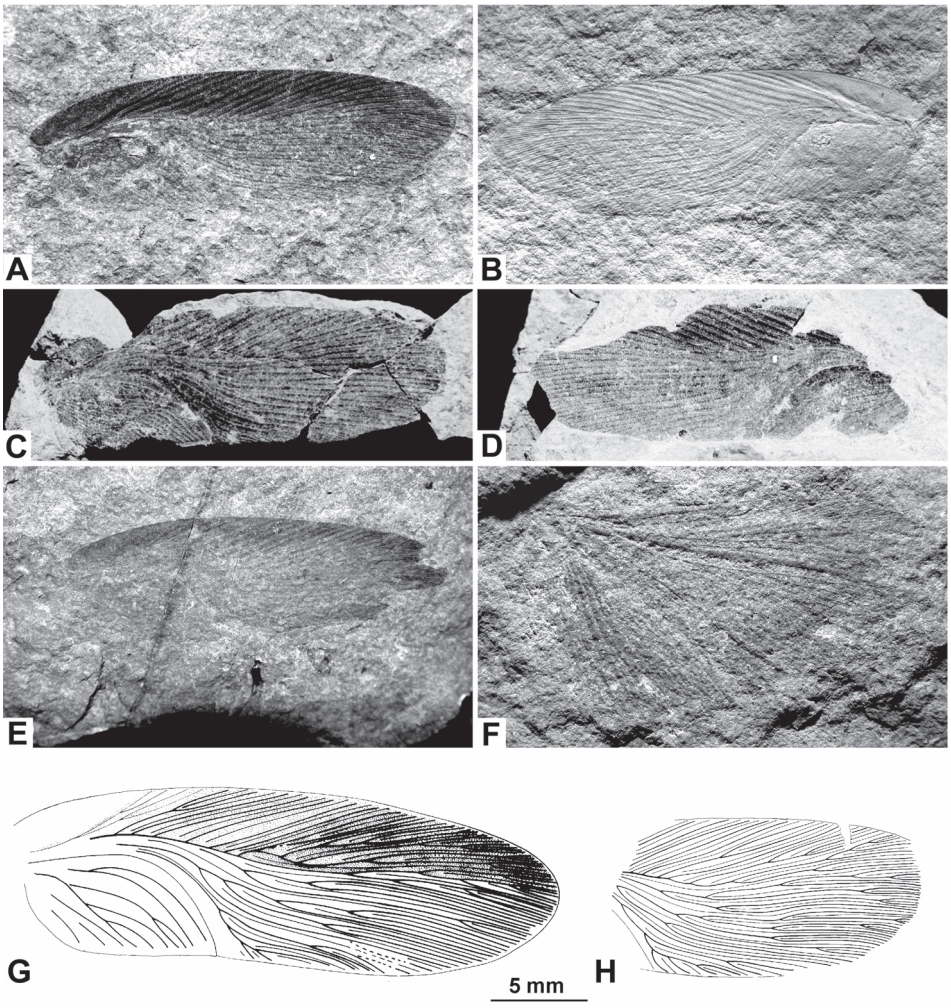

Fig. 2. *Caloblattina mathildae* (Geinitz, 1883): (A, B, G) S 300, forewing, Lower Toarcian of Schandelah near Brunswick (B, covered with ammonium chloride); (C–D) LDA 702, forewing, Lower Toarcian of Dobbertin; (E) G 402-8, holotype of *Palmoblattina gottingensis* Bode, 1953, forewing, Lower Toarcian of Hondelage near Brunswick; (F) G 402-10, holotype of *Polyphleboblatta tenuis* Bode, 1953, hindwing, Lower Toarcian of Hondelage near Brunswick; (H) FGWG 118/1, holotype of *Blattina mathildae* Geinitz, 1883, Lower Toarcian of Dobbertin.

Mesoblattina protypa (Geinitz, 1880)

Fig. 1

Blattina (*Mesoblattina*) *protypa*: Geinitz 1880: 519, fig. 1 [Fw, FGWG 117/1].
Mesoblattina protypa (Geinitz): Handlirsch 1906–08: 428, pl. 40, fig. 19.

Diagnosis: Sclerotised forewings with length about 8 mm; total number of veins at margin (excluding 6–10 A) about 38.

Description: Clavus very short, ending in basal fourth of wing, with fewer than 12 branches. Cu with 5 parallel veins and possibly one additional basal connection to

margin, reaching wing apex. M rich, with about 12 branches, most of which in anterior part; R with 14–18 and possibly more branches. Sc poorly branched.

Holotype (examined): FGWG 117/1, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined: Grimmen: LGA 1320, LGA 1942; Dobbertin: FGWG 219(1), LDA 595, LDA 1086; Mistelgau: M 29, M 73 (all forewings).

Remarks: The crossvein-like fusion of radial veins at the very apex of the wing in the specimen LGA 1942 (Fig. 1E) is an unusual character and has no taxonomic value. Generally, vein fusions are more frequent in the material from Grimmen. This might have been caused by conditions of destabilised ecosystems (Vršanský 2005) within the islands, where the numerous fossils have been found.

Family Caloblattinidae Vršanský & Ansorge in Vršanský, 2000

Type genus: *Caloblattina* Handlirsch, 1906.

Composition: *Aktassoblatta* Vishniakova, 1971; *Asioblatta* Vishniakova, 1968; *Etapia* Vishniakova, 1983; *Euryblattula* Martynov, 1937; *Fusiblatta* Hong, 1980; *Ijablatta* Vishniakova, 1983; *Itchetuja* Vishniakova, 1983; *Kemerowia* Vishniakova, 1983; *Samaroblatta* Tillyard, 1919; *Samaroblattula* Martynov, 1937; *Sogdoblatta* Martynov, 1937; *Soliblatta* Lin, 1986; *Taublatta* Martynov, 1937; *Taublattopsis* Vishniakova, 1985; *Thuringoblatta* Kuhn, 1938, and probably some other insufficiently known genera.

Occurrence: Late Triassic to Late Cretaceous. The latest known representatives are from the Late Cretaceous of Siberia (unpublished material).

Genus *Caloblattina* Handlirsch, 1906

Caloblattina: Handlirsch 1906–08: 430.
Pachyneuroblattina: Handlirsch 1906–08: 433. **Syn. n.**
Apistoblattula: Bode 1953: 115. **Syn. n.**
Strebloblattula: Bode 1953: 116. **Syn. n.**
Palmoblattina: Bode 1953: 116. **Syn. n.**
Macroblattina: Bode 1953: 118. **Syn. n.**
Polyphleboblatta: Bode 1953: 120. **Syn. n.**

Type species: *Blattina mathildae* Geinitz, 1883; Lower Toarcian, Dobbertin, Germany.

Caloblattina mathildae (Geinitz, 1883)

Fig. 2

Blattina mathildae: Geinitz 1883: 29, pl. 6, fig. 1 [Fw, holotype FGWG 118/1, examined].
Caloblattina mathildae (Geinitz): Handlirsch 1906–08: 430, pl. 40, fig. 21.
Pachyneuroblattina rigida: Handlirsch 1906–08: 433, pl. 40, fig. 34 [Fw, holotype FGWG 122/13, examined]. **Syn. n.**
Apistoblattula convexa: Bode 1953: 115, pl. 5, fig. 94 [Fw, holotype Hi 1, examined]. **Syn. n.**
Strebloblattula beienrodensis: Bode 1953: 116, pl. 5, fig. 95 [Fw, SNM W 12]. **Syn. n.**
Palmoblattina gottingensis: Bode 1953: 117, pl. 5, fig. 96 [Fw, holotype G 402-8, examined]. **Syn. n.**
Macroblattina elegans: Bode 1953: 119, pl. 6, fig. 98 [Fw, SNM B 47]. **Syn. n.**
Polyphleboblatta tenuis: Bode 1953: 121, pl. 6, fig. 101 [Hw, holotype G 402-10, examined]. **Syn. n.**
Mesoblattina (?) *grandis*: Bode 1953: 125, pl. 6, fig. 99 [Hw, Cl 106]. **Syn. n.**

Diagnosis: Large species with rich venation and intercalaries that are visible even in poorly preserved material. Total number of veins about 65–75; forewing length about 25 mm; membrane heavily sclerotised.

Description: Forewing 23–30 mm long. Sc richly branched; R with 12–21 and possibly more branches; M with 9–20 veins; Cu with 11 to 22 veins. Clavus with rich venation; A branched, with about 18 branchelets at the margin. Clavus reaching basal third of wing.

Holotype (examined): FGWG 118/1, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined besides the holotypes mentioned in the synonymy list: Dobbertin, LDA 702; Schandelah, S 300.

Remarks: *C. mathildae* is generally a rare species, which is absent from the rich oryctocoenosis of Grimmen. Since there are no taphonomic reasons to explain its absence, it can only be supposed that *C. mathildae* did not live in the source area of the Grimmen insects.

Although forewings of this species have never been found in association with corresponding hindwings, *Polyphleboblatta tenuis* and *Mesoblattina* (?) *grandis*, being 23 mm long, fit well to the forewing size and are regarded as synonyms of *C. mathildae*.

?Raphidiomimidae Vishniakova, 1973

Genus *Liadoblattina* Handlirsch, 1906

Liadoblattina: Handlirsch 1906–08: 428.
Mesoblattopsis: Handlirsch 1906–08: 428. **Syn. n.**
Ptyctoblattina: Bode 1953: 121. **Syn. n.**
Trirhabdoblattina: Bode 1953: 118. **Syn. n.**

Type species: *Mesoblattina blakei* Scudder, 1886; Lower Toarcian, Alderton, England.

Liadoblattina blakei (Scudder, 1886)

Figs 3, 4

Mesoblattina blakei: Scudder 1886: 452, pl. 46, fig. 12 [Fw, holotype NHML I. 3574, examined].
Mesoblattina bensoni: Scudder 1886: 453, pl. 46, fig 17 [Fw, holotype NHML I. 3562, examined]. **Syn. n.**
Mesoblattopsis bensoni (Scudder): Handlirsch 1906–08: 428, pl. 40, fig. 12.
Liadoblattina blakei (Scudder): Handlirsch 1906–08: 428, pl. 40, fig. 17.
(?*Mesoblattina*) *zirkelii*: Handlirsch 1906–08: 435, pl. 40, fig. 39 [Hw, holotype FGWG 121/6, examined]. **Syn. n.**
(?*Mesoblattina*) *polyneura*: Handlirsch 1939: 64, pl. 5, fig. 92 [Hw, holotype FGWG 123/33, examined]. **Syn. n.**
Trirhabdoblattina borealis: Bode 1953: 118, pl. 5, fig. 97 [Fw, SNM B 120]. **Syn. n.**
Ptyctoblattina acuteplicata: Bode 1953: 122, pl. 6, fig. 102 [Hw, SNM W 49]. **Syn. n.**
Ptyctoblattina completa: Bode 1953: 123, pl. 6, fig. 103 [Hw, Hi 9]. **Syn. n.**

Diagnosis: Medium sized, with both wings coloured. Forewings elongated, as much as 3 times as long as wide (length ca. 20 mm). Clavus more than twice as long as wide.

Description: Wings membranous, with distinct coloration. Forewing with simple or weakly branched Sc and narrow costal space; gently curved R with about 15 branches, with M and Cu system developed to same degree (together with some 15 veins); rich A (at or above 10). Numerous cross-veins joined in intercalaries. Diagonal kink present in anal field.

Hindwing with simple Sc, R divided into R1 and RS (10–20 veins); M with up to 5 or more branches; Cu rich with at least 8 veins. A1 reduced compared to other related species, with 2 branches and several blind branches.

Holotype (examined): NHML I. 3574, isolated forewing. ENGLAND: *Gloucesteshire*: Alderton; Upper Lias.

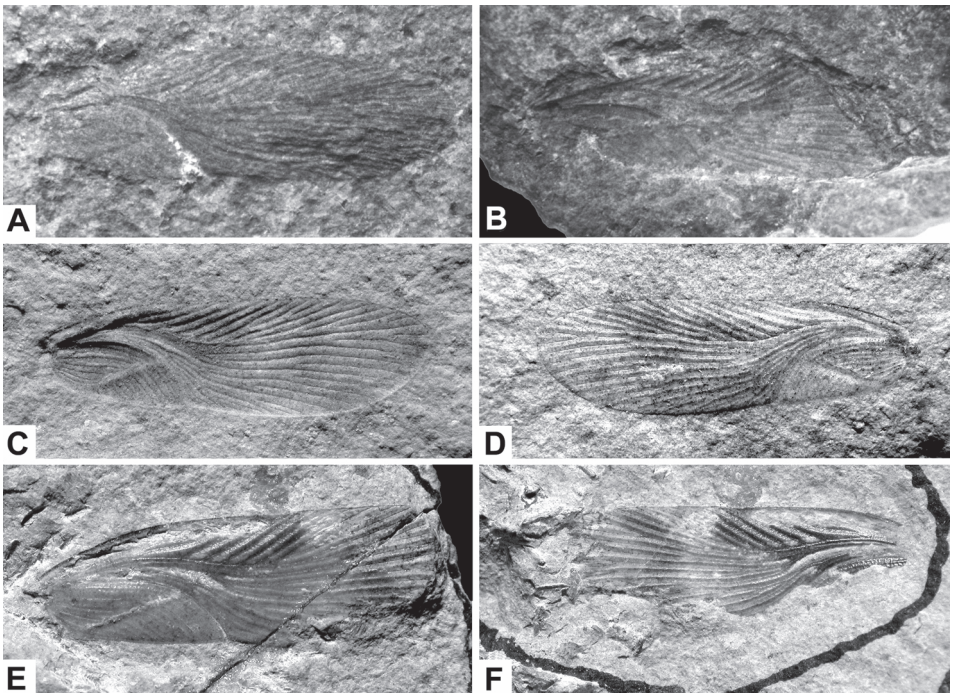

Fig. 3. *Liadoblattina blakei* (Scudder, 1886), photographs of specimens: (A) NHML I. 3562 holotype of *Mesoblattopsis bensoni* (Scudder, 1886), forewing, Upper Lias of Dumbleton, Gloucestershire, England; (B) NHML I. 3574, holotype of *Mesoblattina blakei* Scudder, 1886, Upper Lias of Alderton, Gloucestershire, England; (C–D) FGWG 223, forewing, Lower Toarcian of Dobbertin; (E–F) LDA 336, forewing, Lower Toarcian of Dobbertin.

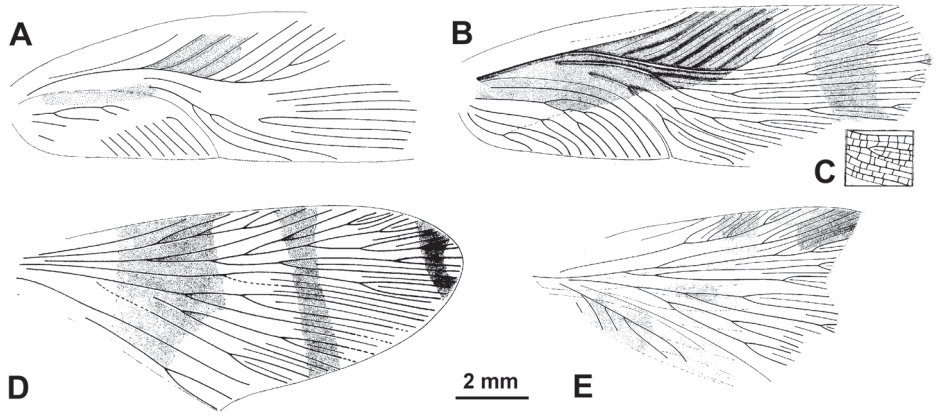

Fig. 4. *Liadoblattina blakei* (Scudder, 1886), details of wing venation: (A) NHML I. 3574, holotype of *Mesoblattina blakei* Scudder, 1886, Upper Lias of Alderton, Gloucestershire, England; (B, C) LDA 336, forewing, Lower Toarcian of Dobbertin (C, detail of intercalary veins); (D) FGWG 121/6, holotype of *Mesoblattina zirkelii* Handlirsch, 1906, hindwing, Lower Toarcian of Dobbertin; (E) FGWG 123/33, holotype of ?*Mesoblattina polyneura* Handlirsch, 1939, hindwing, Lower Toarcian of Dobbertin.

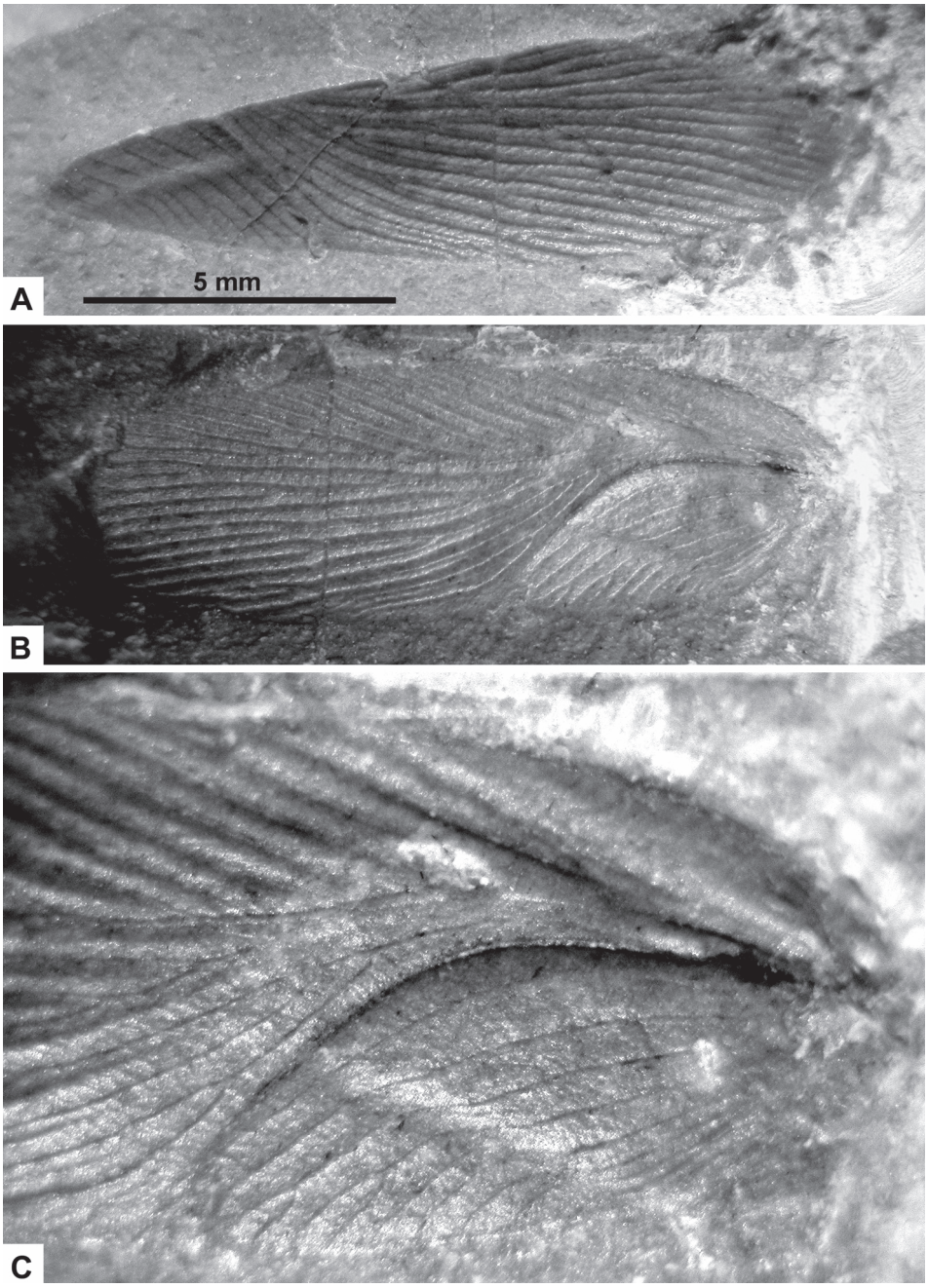

Fig. 5. *Rhipidoblattina geikiei* (Scudder, 1886), holotype NHML I. 10620, I. 11949, forewing, Lower Lias of Browns Wood, Moreton Bagot, Warwickshire, England: (A, B) part and counterpart, (C) clavus at higher magnification.

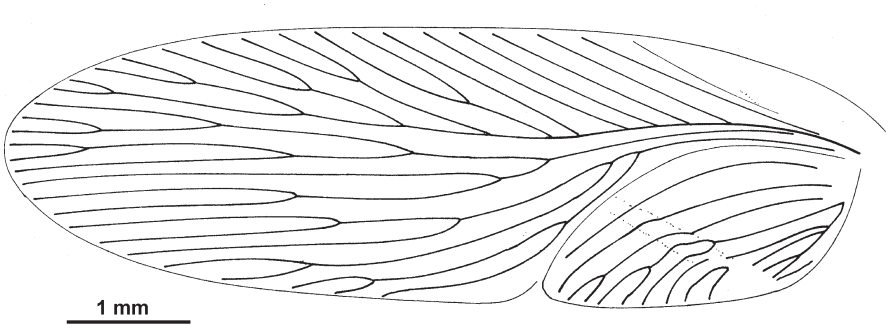

Fig. 6. *Rhipidoblattina geikiei* (Scudder, 1886), holotype, details of forewing venation.

Additional material besides the holotypes mentioned in the synonymy list examined: Dobbertin, Fw LDA 336, FGWG 223 (2); Schandelah, Fw S3-14; Holzmaden H 5, H 29, forewings.

Remarks: A1 in the hindwing seems to be formed similarly to that in Blattulidae. The taxon appears to be rather advanced, probably with actively flying individuals. Although never found associated with forewings, it is supposed that the similarly coloured hindwings, listed in the above synonymy, represent hindwings of *Liadoblattina blakei*. With a length of about 15 mm they fit well to the forewing size.

The coloration could serve as disruptive markings against visually adept predators (see Jarzembowski 1994).

Caloblattinoidea fam. n.
Genus *Rhipidoblattina* Handlirsch, 1906
Rhipidoblattina geikiei (Scudder, 1886)

Figs 5, 6

Mesoblattina geikiei: Scudder 1886: 454, pl. 46, fig. 9.
Rhipidoblattina geikiei (Scudder): Handlirsch 1906–08: 429, pl. 40, fig. 20; 1939: 57, pl. 4, fig. 72.

Diagnosis: Forewing length 13.7 mm. Total number of veins at margin about 45–50. Clavus short.

Description: Wing margins more or less parallel; venation regular with reticulations between veins. Sc field shorter than clavus, with Sc 2- or possibly 3-branched. R slightly concave with most branches simple, rarely tertiary branched, with 16 veins at margin. M rich with 9 branches; Cu expanded, with 8 branches. Faint intercalaries present (Fig. 5C). Clavus comparatively short with 12 or 13 anal veins that are branched (A1–2 simple) with diagonal kink.

Holotype (examined): Isolated forewing, part and counterpart, NHML I. 10620, I. 11949. ENGLAND: *Warwickshire*: Browns Wood, Moreton Bagot; Lower Lias.

Blattaria *incertae familiae*
Genus *Eublattula* Handlirsch, 1939
Eublattula crassivena Handlirsch, 1939

Fig. 7

Eublattula crassivena: Handlirsch 1939: 63, pl. 5, fig. 91.

Diagnosis: Forewing more than 10 mm long, with thick branches and deeply curved R not reaching wing apex. Clavus with diagonal kink.

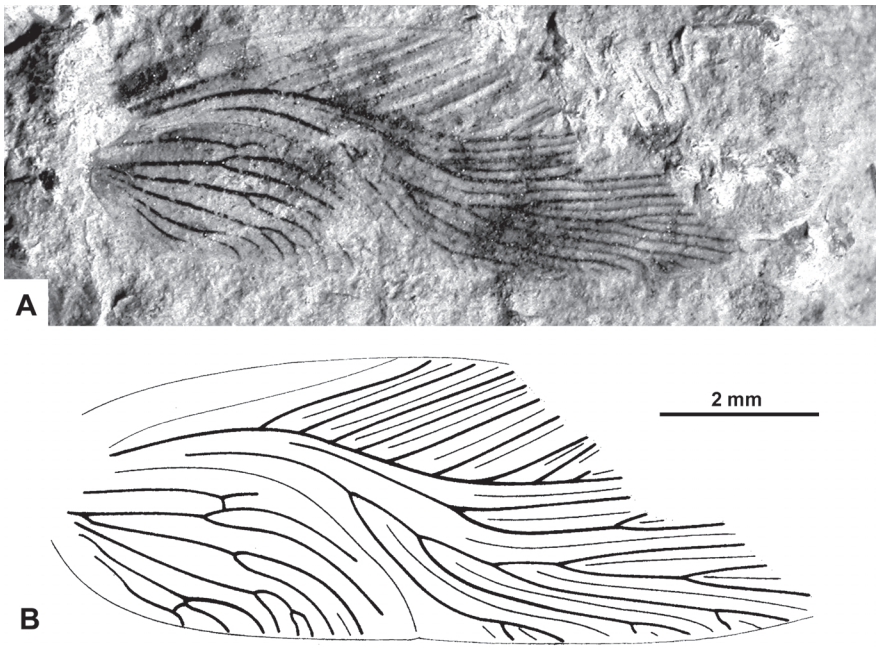

Fig. 7. *Eublattula crassivena* Handlirsch, 1939, holotype FGWG 123/32, Lower Toarcian of Dobbertin: (A) photograph of specimen, (B) details of venation.

Description: Wing with very strong venation, 11–13 mm long (distal part of wing broken), kinked clavus overlapping basal third of wing, with about 11 veins and abundant fusions; Cu expanded (6–10 veins), almost reaching wing apex. M reduced to several branches. R curved with about 10 branches. Sc simple, forked.

Holotype (examined): FGWG 123/32, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Remarks: According to the vein branchings, the taxon seems to be a stem group member of the Blattulidae, or to belong to the Liberiblattinidae Vršanský, 2002.

Superfamily ?Polyphagoidea Walker, 1868
Family Blattulidae Vishniakova, 1982
Genus *Blattula* Handlirsch, 1906

Blattula: Handlirsch 1906–08: 431.
Mesoblattula: Handlirsch 1906–08: 430. **Syn. n.**
Parablattula: Handlirsch 1920: 191. **Syn. n.**
Peloblattula: Handlirsch 1939: 60. **Syn. n.**
Metablattula Handlirsch 1939: 61. **Syn. n.**
Chiloblattula: Handlirsch 1939: 61. **Syn. n.**
Ectinoblattula: Handlirsch 1939: 62. **Syn. n.**
Englyptoblatta: Bode 1953: 119. **Syn. n.**

Type species: *Blattina dobbertinensis* Geinitz, 1884 (designated by Becker-Migdisova 1962: 103) is now considered a junior synonym of *Blattula langfeldti* (Geinitz, 1880).

Remarks: Although the name *Mesoblattula* Handlirsch, 1906 has page priority over *Blattula* Handlirsch, 1906, we use the right of the first reviser to treat the name

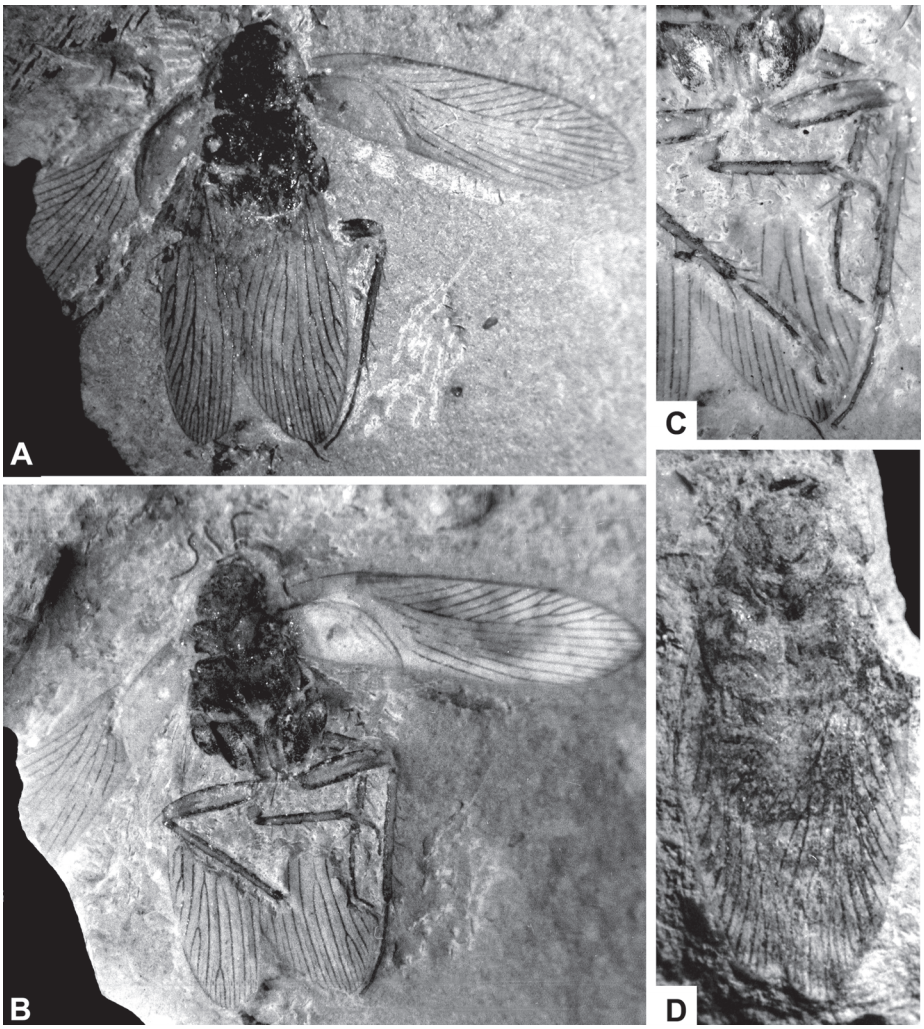

Fig. 8. *Blattula langfeldti* (Geinitz, 1880): (A–C) LGA 1820, Lower Toarcian of Grimmen: (A) total before preparation of legs, (B) after preparation of legs and antennae, (C) details of legs; (D) LDA 96, Lower Toarcian of Dobbertin.

Mesoblattula as a junior subjective synonym of *Blattula*. *Blattula* is very similar in wing venation to the mainly Lower Cretaceous *Elisama* Giebel, 1856. The most striking difference is a dark macula in *Elisama* forewings.

Blattula langfeldti (Geinitz, 1880)

Figs 8–15

Blattina langfeldti: Geinitz 1880: 521, fig. 3 [Fw, holotype FGWG 117/20, examined].
Blattina nana: Geinitz 1883: 30, pl. 22, fig. 2 [Hw, holotype FGWG 118/3, examined]. **Syn. n.**
Blattina (*Mesoblattina*) *dobbertinensis*: Geinitz 1884: 570, pl. 13, fig. 1 [Fw, holotype FGWG 119/2, examined]. **Syn. n.**
Blattina incerta: Geinitz 1884: 571, pl. 13, fig. 2 [Hw, holotype FGWG 119/2, examined]. **Syn. n.**

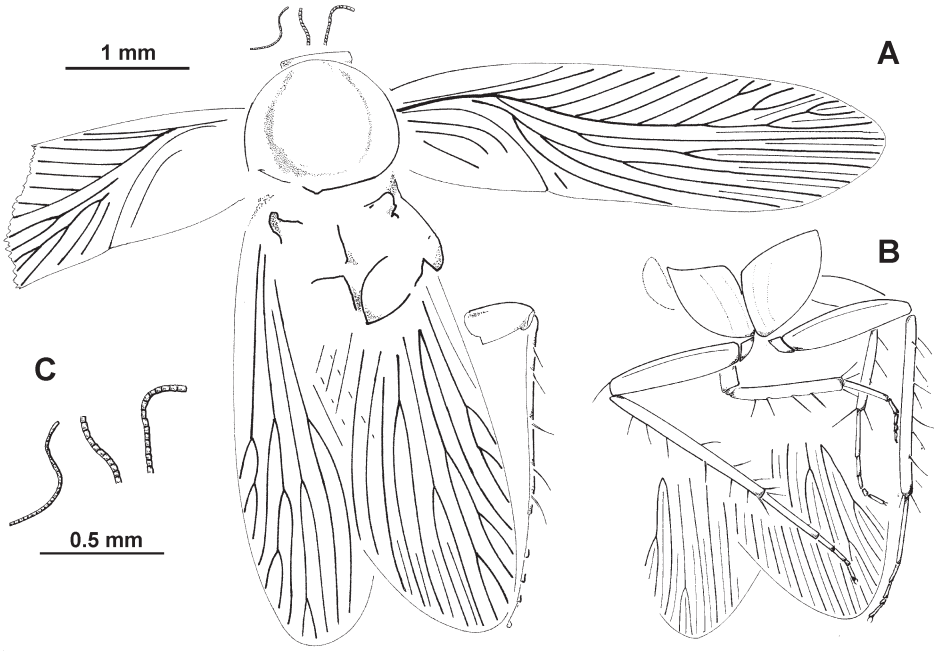

Fig. 9. *Blattula langfeldti* (Geinitz, 1880), LGA 1820, Lower Toarcian of Grimmen: (A) details of specimen before preparation of legs, (B) details of legs after preparation, (C) details of antennae.

Dipluroblattina scudderi: Geinitz 1887: 200, pl. 5, fig. 7 [Fw, holotype FGWG 120/2, examined]. **Syn. n.**
Ctenoblattina langfeldti (Geinitz): Scudder 1886: 443.
Mesoblattina dobbertinensis (Geinitz): Scudder 1886: 455.
Mesoblattula dobbertiniana: Handlirsch 1906–08: 430, pl. 40, fig. 23 [Fw, holotype FGWG 122/103, examined]. **Syn. n.**
Mesoblattula geinitziana: Handlirsch 1906–08: 430, pl. 40, fig. 24 [Fw, holotype FGWG 122/10-11, examined]. **Syn. n.**
Blattula dobbertinensis (Geinitz): Handlirsch 1906–08: 431, pl. 40, fig. 25.
Blattula langfeldti (Geinitz): Handlirsch 1906–08: 431, pl. 40, figs 26, 27.
Blattula ancilla: Handlirsch 1906–08: 431, pl. 40, fig. 28 [Fw, holotype FGWG 122/12, examined]. **Syn. n.**
Blattula geinitzi: Handlirsch 1906–08: 432, pl. 40, fig. 29 [Fw, probably lost]. **Syn. n.**
Battula scudderi (Geinitz): Handlirsch 1906–08: 432, pl. 40, fig. 30.
?*Blattula incerta* (Geinitz): Handlirsch 1906–08: 432, pl. 40, fig. 31.
?*Blattula debilis*: Handlirsch 1906–08: 433, pl. 40, fig. 32. **Syn. n.**
?*Blattula pusillima*: Handlirsch 1906–08: 433, pl. 40, fig. 33 [Hw, holotype FGWG 122/250, examined]. **Syn. n.**
(?*Mesoblattina*) *nana* (Geinitz): Handlirsch 1906–08: 435, pl. 40, fig. 38.
Parablattula reticulata: Handlirsch 1920: 191, fig. 153 [Fw, holotype FGWG 123/26, examined]; 1939: 61, pl. 5, fig. 83. **Syn. n.**
?*Mesoblattula ala*: Handlirsch 1939: 58, pl. 4, fig. 74 [Hw, holotype FGWG 123/45, examined]. **Syn. n.**
Blattula riparia: Handlirsch 1939: 58, pl. 4, fig. 75 [Fw, holotype FGWG 123/20, examined]. **Syn. n.**
Blattula intercalata: Handlirsch 1939: 58, pl. 4, fig. 76 [Fw, holotype FGWG 123/21, examined]. **Syn. n.**
Blattula brunneri: Handlirsch 1939: 59, pl. 5, fig. 77 [Fw, holotype FGWG 123/22, examined]. **Syn. n.**
?*Blattula vicina*: Handlirsch 1939: 59, pl. 5, fig. 79 [Fw, holotype FGWG 123/23, examined]. **Syn. n.**
?*Blattula acutipennis*: Handlirsch 1939: 59, pl. 5, fig. 80 [Hw, NHMW 1984/33/11]. **Syn. n.**
Peloblattula oligoneura: Handlirsch 1939: 60, pl. 5, fig. 81 [Fw, holotype FGWG 123/24, examined]. **Syn. n.**
Parablattula simplicissima: Handlirsch 1939: 60, pl. 5 fig. 82 [Fw, holotype FGWG 123/25, examined; counterpart NHMW 1984/33/12]. **Syn. n.**
Metablattula lipomena: Handlirsch 1939: 61, pl. 5, fig. 84 [Fw, holotype FGWG 123/27, examined]. **Syn. n.**
Chiloblattula simplex: Handlirsch 1939: 61, pl. 5, fig. 85 [Fw, holotype FGWG 123/28, examined]. **Syn. n.**
?*Chiloblattula subcostalis*: Handlirsch 1939: 62 [Hw, holotype FGWG 123/29, examined]. **Syn. n.**

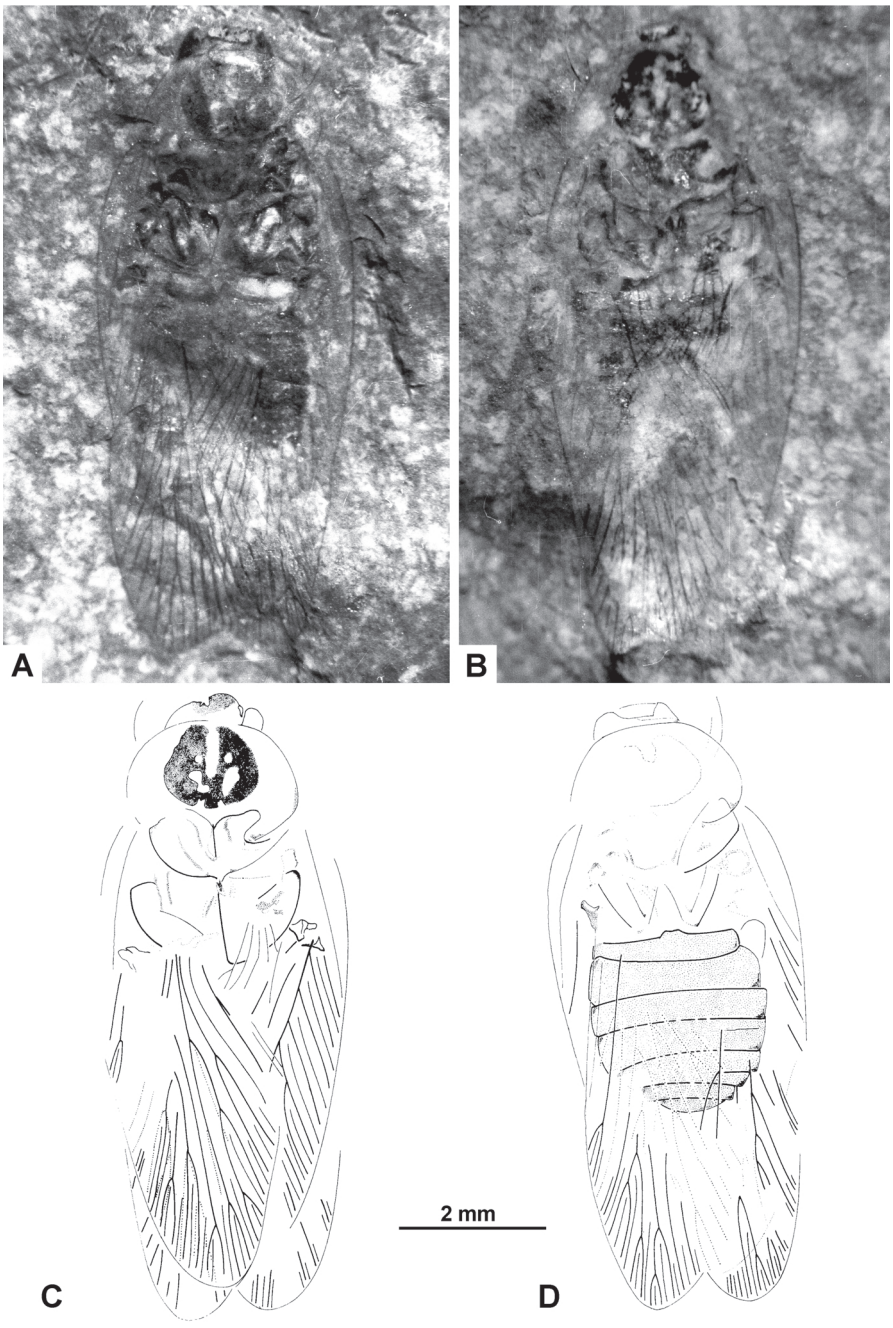

Fig. 10. *Blattula langfeldti* (Geinitz, 1880), LGA 888/1-2, Lower Toarcian of Grimmen: (A, B) photographs of part and counterpart, (C, D) details of body structures.

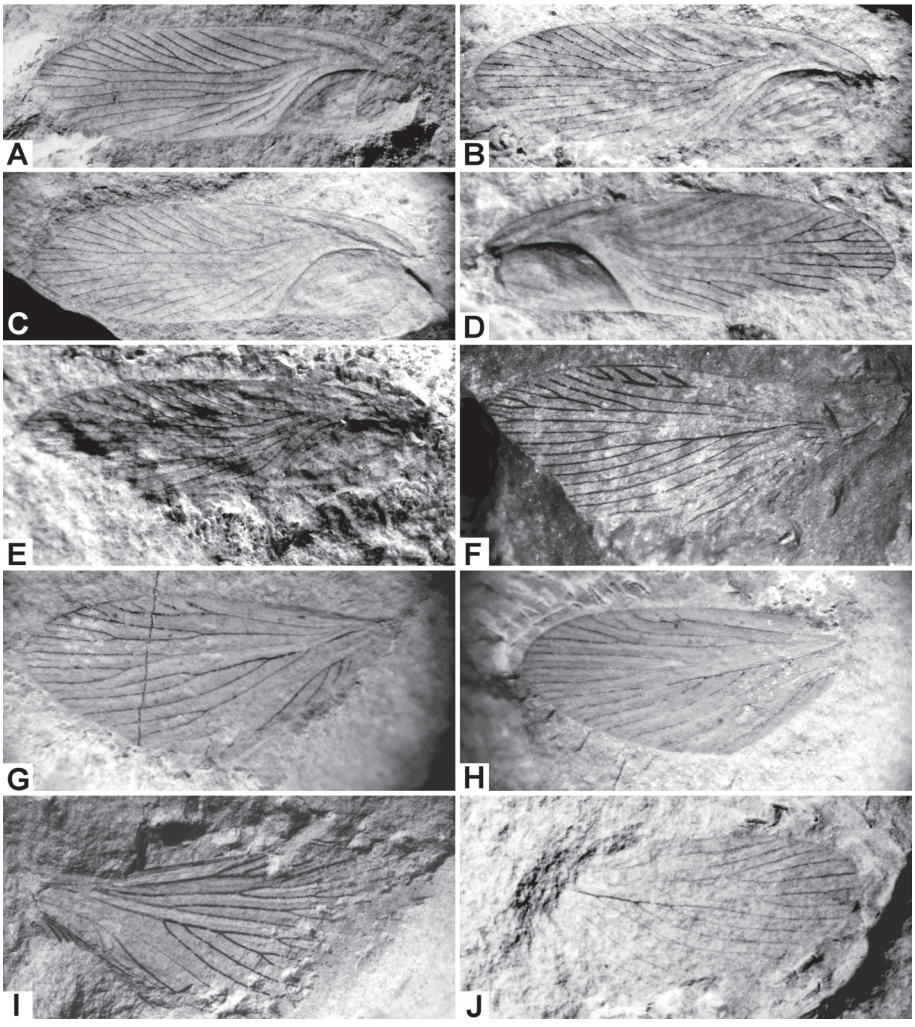

Fig. 11. *Blattula langfeldti* (Geinitz, 1880): (A) FGWG 123/26, forewing, holotype of *Parablattula reticulata* Handlirsch, 1939, Dobbertin; (B) LDA 7, forewing, Dobbertin; (C) LDA 66, forewing, Dobbertin; (D) LGA 2356, forewing, Grimmen; (E) LDA 586, forewing, Dobbertin; (F) LGA 96, hindwing, Grimmen; (G) LGA 1275, hindwing, Grimmen; (H) LGA 2507, hindwing, Grimmen; (I) LGA 380, hindwing, Grimmen; (J) LDA 85, hindwing, Dobbertin.

?*Chiloblattula longipennis*: Handlirsch 1939: 62, pl. 5, fig. 86 [Hw, holotype FGWG 123/30, examined]. **Syn. n.**
Ectinoblattula medialis: Handlirsch 1939: 63, pl. 5, fig. 90 [Fw, holotype FGWG 123/57, examined]. **Syn. n.**
Blattula hattorfensis: Bode 1953: 114, pl. 5, fig. 93 [Fw, SMN W 13]. **Syn. n.**
Englyptoblatta elegantula: Bode 1953: 120, pl. 6, fig. 100 [Fw, SNM W 9/11]. **Syn. n.**
Elisama langfeldti (Geinitz): Ansorge 2003: 296, fig. 2B.
Blattula langfeldti (Geinitz): Ansorge 2004: 782, fig. 2.

Diagnosis: Forewing: length 6.5–9 mm; Sc 1, R 8–14, M 2–7, Cu 4–10, A 5–12. Hindwing: length 6.5–7.5 mm; Sc 1, R 3–4+3–5, M 2–3, Cu 6–8.

Description: Pronotum ovoid in shape, transverse, with distinct coloration. Forewing length 6.5–9 mm, width about 2.3 mm; Sc simple, rarely with some weak lateral

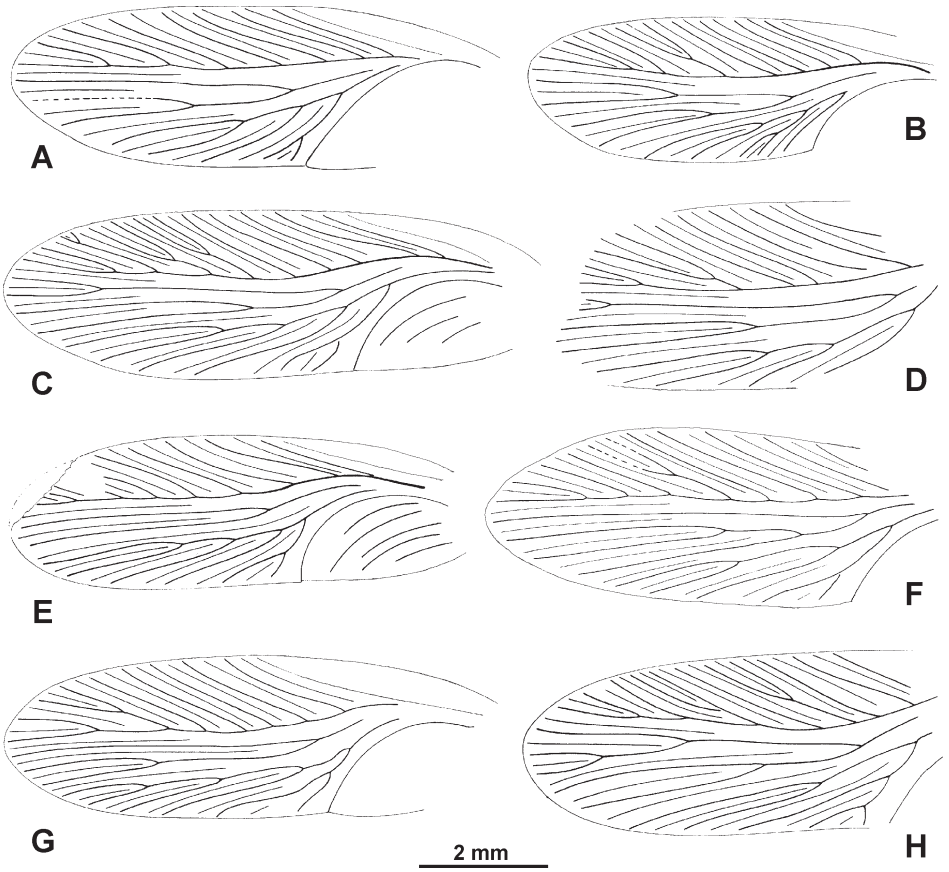

Fig. 12. *Blattula langfeldti* (Geinitz, 1880), details of venation of forewings, Lower Toarcian of Dobbertin and Grimmen: (A) FGWG 122/12, holotype of *Blattula ancilla* Handlirsch, 1906; (B) LGA 880; (C) FGWG 123/26, holotype of *Parablattula reticulata* Handlirsch, 1920; (D) FGWG 123/25, holotype of *Parablattula simplicissima* Handlirsch 1939; (E) FGWG 123/28, holotype of *Chiloblattula simplex* Handlirsch, 1939; (F) FGWG 123/27, holotype of *Metablattula lipomena* Handlirsch, 1939; (G) FGWG 119/2, holotype of *Blattula dobbertinensis* (Geinitz, 1884); (H) FGWG 122/103, holotype of *Mesoblattula dobbertiniana* Handlirsch, 1906.

branchlets; R with 8–14 veins; M with 2–7 branches; Cu with 4–10 branches. A reticulate, with 5–12 veins reaching margin, veins in clavus may be reticulate. Hindwing length 6.5–7.5 mm with Sc simple; R divided near base into R with 3–4 veins and RS with 3–5 veins; M with 2 or 3 branches; CuA with 6–8 veins. Legs thin, with sparse, long and thin spines.

Holotype (examined): FGWG 117/20, isolated forewing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined: Besides the re-studied holotypes described by Geinitz and Handlirsch from the Lower Toarcian of Dobbertin and listed in the synonymy, the following additional material is in Ansorge's collection. Hindwings: LDA 40; 76; 85; 86; 109; 455; 485; 594/3; 660/1, 2; 593/3; LGA 86; 96; 275; 331/1, 2; 380; 425; 579; 594; 888; 893; 1077; 1201; 1275; 1372; 1529; 1578; 1739; 1820; 2169. Forewings: LDA 7, 66; 169; 240; 145; 254; 289; 326; 348; 581; 586; 629; 611; 798; 869; 910; 1017; 2196; LGA 13; 118; 154; 880; 1328; 1435; 1519; 1842; 1887; 1926; 2006; 2015; 2196; 2356, S 137; 139. Complete specimens:

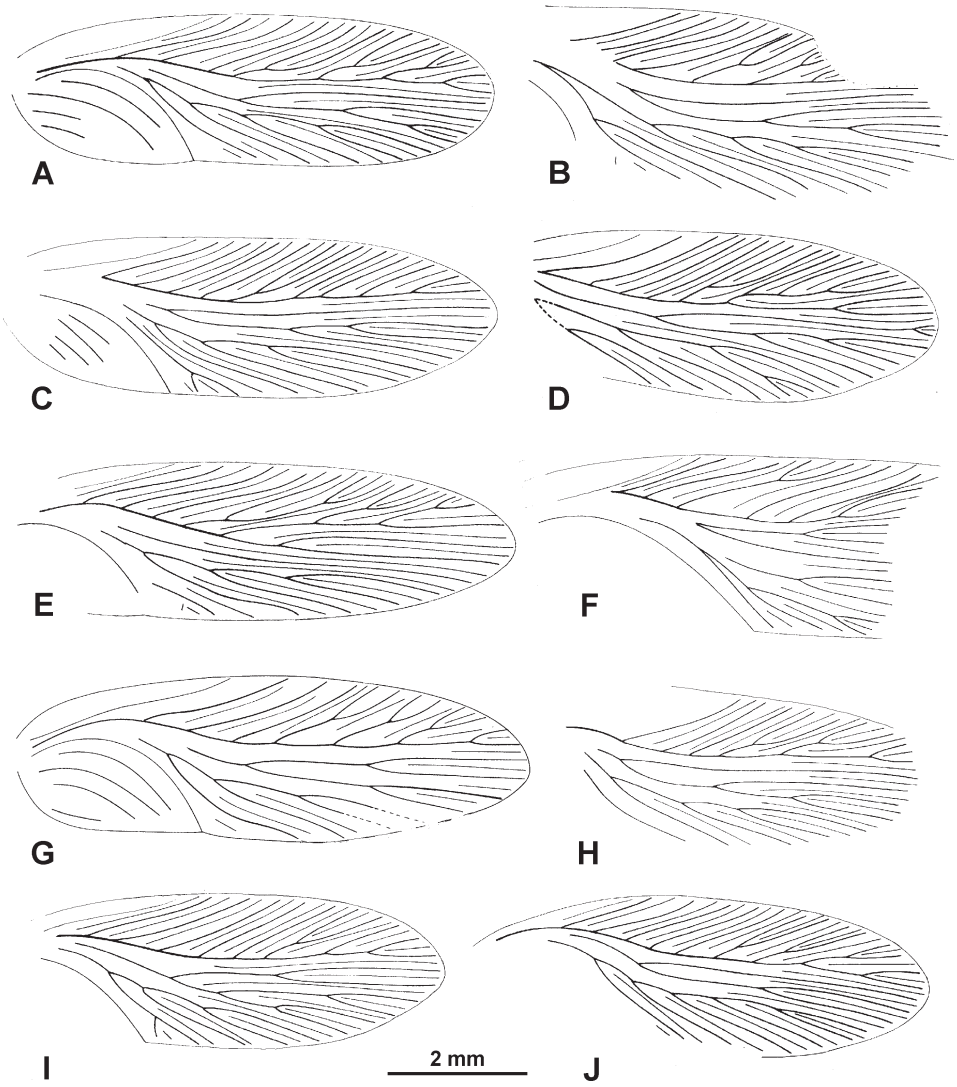

Fig. 13. *Blattula langfeldti* (Geinitz, 1880), details of venation of forewings, Lower Toarcian of Dobbertin, Grimmen (LGA 2356) and Schandelah (S 139): (A) FGWG 123/21, holotype of *Blattula intercalata* Handlirsch, 1939; (B) FGWG 120/2, holotype of *Dipluroblattina scudderi* Geinitz, 1887; (C) FGWG 123/20, holotype of *Blattula riparia* Handlirsch, 1939; (D) FGWG 117/20, holotype of *Blattina langfeldti* Geinitz, 1880; (E) FGWG 123/57, holotype of *Ectinoblattula medialis* Handlirsch, 1939; (F) FGWG 122/10-11, holotype of *Mesoblattula geinitziana* Handlirsch, 1906; (G) LGA 2356; (H) S 139; (I) FGWG 123/24, holotype of *Peloblattula oligoneura* Handlirsch, 1939; (J) FGWG 123/22, holotype of *Blattula brunneri* Handlirsch, 1939.

LDA 96; LGA 888; 1820. Two species described by Bode (1953) from the Lower Toarcian of Hattorf (Lower Saxony) have not been re-examined.

Note: A few complete specimens with associated fore- and hindwings allow us to determine isolated fore- and hindwings.

Variability (Tables 2, 3): Both complete specimens from Grimmen show considerable variation between the left and right wings. Sc is stable, simple in all wings. Other veins

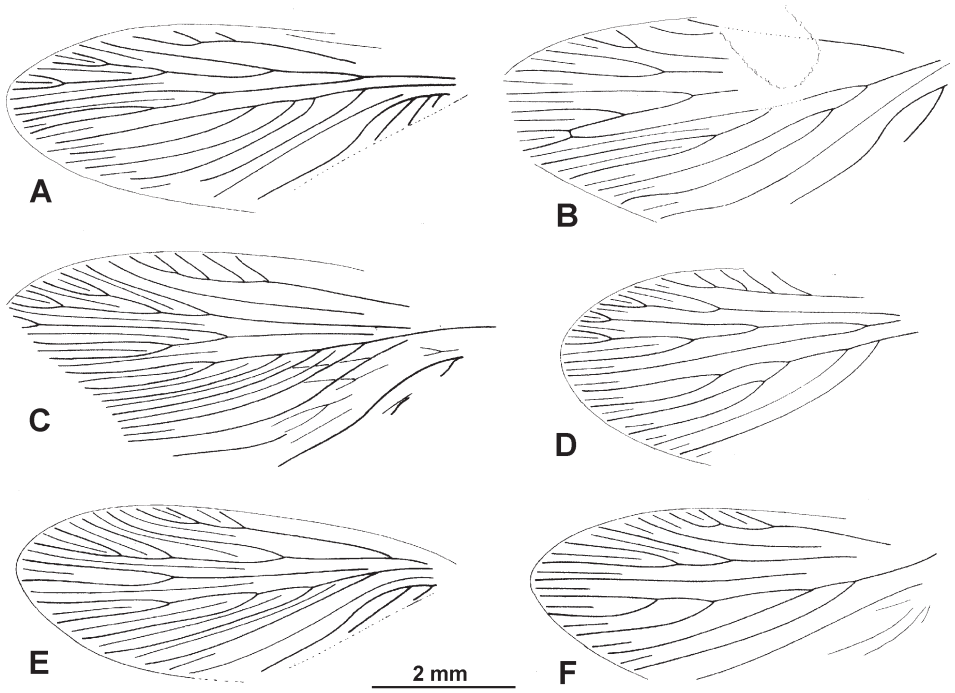

Fig. 14. *Blattula langfeldti* (Geinitz, 1880), details of venation of hindwings, Lower Toarcian of Dobbertin (FGWG) and Grimmen (LGA): (A) FGWG 123/23, holotype of ?*Blattula vicina* Handlirsch, 1939; (B) LGA 579; (C) LGA 96; (D) LGA 893; (E) FGWG 123/30, holotype of ?*Chiloblattula longipennis* Handlirsch, 1939; (F) FGWG 122/250, holotype of ?*Blattula pusillima* Handlirsch, 1906.

vary. Hindwing variation, considered as more stable, is expressed in the varying number of RS branches (4 in left wing; 5 in right wing), while R is stable in this case (3). M is 3-branched in the left wing, and 2-branched in the right wing. Unfortunately, the wings are not complete, so it is uncertain whether the Cu will compensate differences in the total vein number (6 in right wing, and evidently more than 3 in the left wing).

TABLE 2

Variability of the forewings of *Blattula langfeldti*. SUM designates the total number of all veins, except for A, at wing margin.

	size, mm	Cu	M	R	R+M	Cu+M	R+Cu	SUM
Sample size (n)	44	44	44	44	43	43	39	42
Minimum	6.4	4	1	6	11	7	12	17
Maximum	9.0	10	9	15	19	16	23	28
Median	7	6	4	11	15	10	17	22
Mode	7	6	4	11	14	9	19	22
Standard error	0.10	0.19	0.21	0.30	0.32	0.29	0.39	0.38
Standard deviation	0.63	1.23	1.40	1.96	2.05	1.90	2.44	2.47
Variance	0.40	1.52	1.95	3.85	4.19	3.61	5.98	6.09
Coefficient of variation	8.71	20.06	33.58	18.22	13.73	18.37	14.51	11.24

TABLE 3

Variability of the hindwing of *B. langfeldti*. SUM designates the total number of all veins (only remigial veins are counted; R is R1+RS) at wing margin.

	size, mm	Cu	M	R	R1	RS	R+M	Cu+M	R+Cu	SUM
Sample size	24	31	32	28	34	30	28	30	27	22
Minimum	6	5	1	4	2	2	8	6	10	14
Maximum	8	8	6	11	5	6	15	13	18	22
Median	7	6	3	7	3	4	10	9	14	17
Mode	7	6	3	7	3	4	10	9	15	18
Standard error	0.08	0.15	0.17	0.25	0.14	0.15	0.35	0.28	0.33	0.51
Standard deviation	0.38	0.85	0.98	1.32	0.82	0.83	1.84	1.53	1.73	2.39
Variance	0.14	0.72	0.97	1.74	0.67	0.69	3.37	2.35	2.98	5.73
Coefficient of variation	5.41	13.81	32.79	17.50	24.16	19.40	17.42	16.73	12.46	13.86

The variability studies of *B. langfeldti* revealed some general principles regarding the control of the cockroach wing venation development. With the increasing number of veins in a competent venational complex, the variability falls (coefficient of variation (CV) is lower). Therefore we have also analysed the dependence of the CV according to the number of veins. Results show that the CV is comparatively low in the competent venational systems (R, M, Cu), higher in neighbouring venational complexes and the highest between complexes that are not neighbouring (in the forewing of *B. langfeldti* it is low in (R+M) complex, high in (R) and (Cu); in the hindwing, the most apparent is the relatively high variability of (R+Cu) complex). That means that the control mechanisms are developed autonomically, "working best" in each venational complex (R, M, Cu) (each major branch has its own control mechanism) but these separate systems communicate with their surroundings, and influence each other (see Schneider 1977, 1978*a*).

Remarks: There is no gap in the variability of the venation which would suggest dimorphism in the flight abilities of both sexes.

Blattula dubia (Handlirsch, 1939), **comb. n.**

Fig. 16

?*Chiloblattula dubia*: Handlirsch 1939: 62, pl. 5, fig. 89.

Diagnosis: One of smallest known blattulids, with forewing length 4.5–6 mm and venation reduced to some 20 veins.

Description: Forewing with venation reduced to some 20 veins. R with about 7 veins; M with about 3; Cu with about 4. Hindwing with R1 and RS (3–5+3–5); M with 2 or 3 branches; Cu with 4–5+1 branches; A1 with at least two branches.

Holotype (examined): FGWG 123/31, isolated hindwing. GERMANY: *Mecklenburg*: former clay pit of Schwinz, near Dobbertin; carbonate concretions of the marine "Green Series" clay, Lower Toarcian, *exaratum* Subzone.

Additional material examined: Dobbertin, hindwing LDA 304/1; Grimmen, forewing LGA 1725.

Remarks: The species differs from *B. langfeldti* in having a rounded forewing margin and in having more reduced venation, which results from the smaller size of this species.

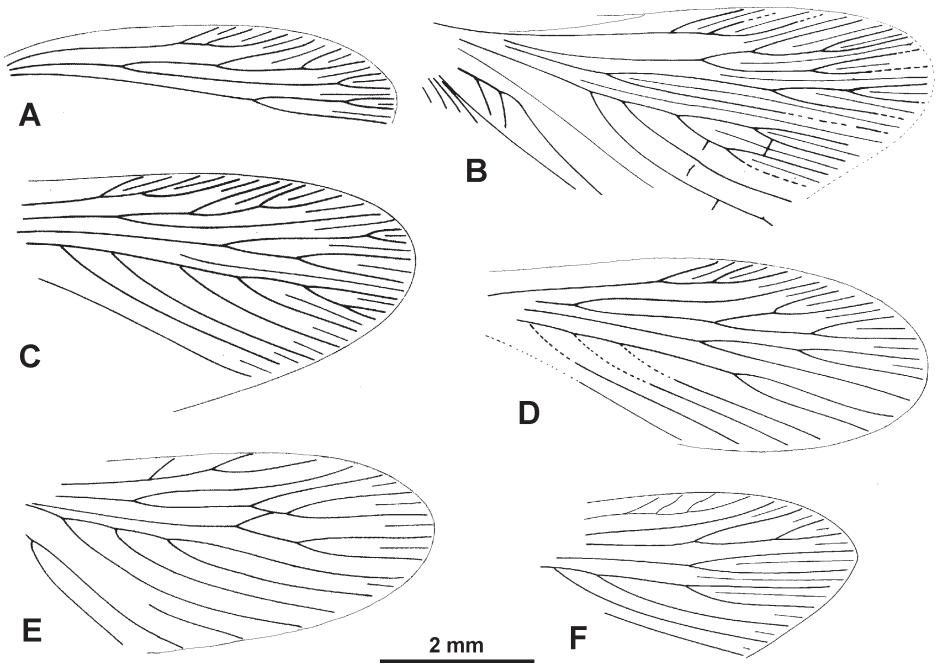

Fig. 15. *Blattula langfeldti* (Geinitz, 1880), details of venation of hindwings, Lower Toarcian of Dobbertin and Grimmen (LGA 380): (A) FGWG 123/45, holotype of ?*Mesoblattula ala* Handlirsch, 1939; (B) LGA 380; (C) FGWG 118/3, holotype of *Blattina nana* Geinitz, 1883; (D) FGWG 119/2, holotype of *Blattina incerta* Geinitz, 1884; (E) LDA 85; (F) FGWG 123/29, holotype of ?*Chiloblattula subcostalis* Handlirsch, 1939.

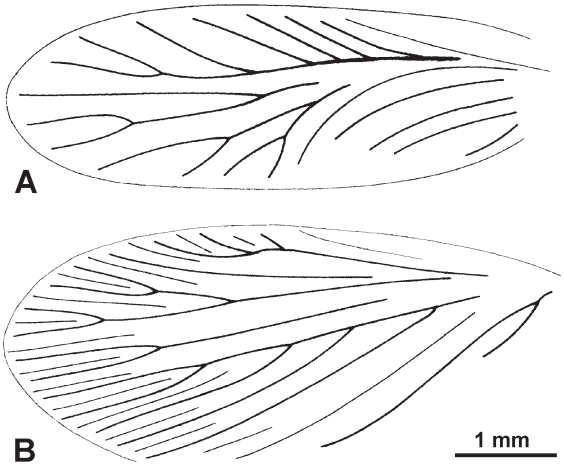

Fig 16. *Blattula dubia* (Handlirsch, 1939), wing venation: (A) LGA 1725, forewing, Lower Toarcian of Grimmen; (B) FGWG 123/31, hindwing, holotype of ?*Chiloblattula dubia* Handlirsch, 1939, Lower Toarcian of Dobbertin.

Although not found in association with a hindwing, a very small isolated forewing LGA 1725 from Grimmen most likely belongs to this species.

DISCUSSION

Cockroaches from the Lower Toarcian marine insect oryctocoenoses are mainly represented by isolated wings and wing fragments, e.g., isolated anal fields. *B. langfeldti*, the most common cockroach in Grimmen and Dobbertin, is known from three complete specimens. The record of few articulated specimens and a similar number of fore- and hindwings indicates that representatives of this species were capable fliers. In accordance with the supposed close position of the depositional realm of the Grimmen and Dobbertin insects to a shore line, we see a reason that this species is rather rare in the other localities, which were thought to have been further offshore.

The large *C. mathildae* and *L. blakei* are absent from Grimmen, which may indicate that these species did not live in the source area (islands) of the Grimmen insects. Otherwise, the composition of the insect fauna in marine oryctocoenoses is definitely controlled by taphonomic factors and it depends primarily on the distance to the shoreline.

Taxonomic work is made difficult by increasing complexity within the systematics of this order. Our observations are based on investigations of Vishniakova (1983), Schneider (1977, 1978*a*, *b*, 1980*a*, *b*, 1983, 1984), Schneider and Werneburg (1993) and ourselves. The taxonomic and systematic position of the Mesoblattinidae, differing from Caloblattinidae is now fully recognised, based on the apparent difference in size, general habitus, terminalia and venational characters.

The diversity of the studied Lower Toarcian cockroaches is low, most probably as a result of the island character within the source area. Blattulidae are represented only by two species, with *B. langfeldti* dominant (88 specimens) and with higher variability compared with the Lower Cretaceous Blattulidae of the same size and having the same number of veins. Both sexes shared a similar habitus and do not differ significantly in the size or form.

Very little is known about the niches of fossil cockroaches, but all the studied cockroaches appear to be saprophagous, although in Jurassic *Liadoblattina* from Asia, lengthening of the body and wings may suggest a predatory habit as in Upper Jurassic Raphidiomimidae Vishniakova, 1973 and in mantises (Vršanský 1999*a*, 2002).

Unlike the most common *B. langfeldti* and other representatives of the family Blattulidae, the wing structure of the largest *Caloblattina* species suggests that representatives of the species were not active fliers. Other species belonging to the Blattulidae have been found together with apparently diurnal Umenocoleidae in coprolites from Mongolia (Vršanský 2003). Thus it is likely that the most common Blattulidae were also diurnal.

ACKNOWLEDGEMENTS

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Nymphs of a new family Neazoniidae fam. n. (Hemiptera: Fulgoromorpha: Fulgoroidea) from the Lower Cretaceous Lebanese amber

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ABSTRACT

New species of extinct Fulgoroidea from the Lower Cretaceous Lebanese amber, *Neazonia tripleta* sp. n., *Neazonia immatura* sp. n., and *Neazonia imprinta* sp. n., are described as members of a new genus *Neazonia* gen. n. Descriptions are based on a IIIrd instar nymph, the exuvium of a Vth instar nymph and a cast in amber of a probable IIIrd instar nymph. The new extinct family Neazoniidae fam. n. is established for these fossils. Morphological characters and their importance in reconstructing evolutionary patterns of Fulgoroidea are discussed.

KEY WORDS: Hemiptera, Fulgoroidea, Neazoniidae, Lebanese amber, Lower Cretaceous, nymphs, morphology, coevolution, new taxa.

INTRODUCTION

The Fulgoroidea is a highly variable group of the Hemiptera and consists of two extinct (Fulgoridiidae and Lalacidae) and 21 currently recognised extant families. The recognised family groups include extant Achilidae+Achilixiidae, Caliscelidae, Cixiidae, Delphacidae, Derbidae, Dictyopharidae, Eurybrachidae+Gengidae, Flatidae+ Hypochthonellidae, Fulgoridae, Issidae+Acanaloniidae, Kinnaridae+Meenoplidae, Lophopidae, Nogodinidae, Ricaniidae, Tettigometridae, Tropiduchidae. The taxonomic status of some of these is not resolved. Achilixiidae used to be treated as representatives of a distinct family (Wilson 1989); they have since been included in Achilidae as subfamilies Achilixiinae and Bebaiotinae by Emeljanov (1991), or recently moved to Cixiidae, as proposed by Liang (2002). Kinnaridae appears to be a paraphyletic unit within the Meenoplidae (Bourgoin 1993). Gengidae could be united with Eurybrachidae, and Hypochthonellidae with Flatidae (O'Brien 2002). Issidae have recently been redefined, with Caliscelidae recognised as a distinct family (Emeljanov 1999). Acanaloniidae have been subsumed within Issidae (Fennah 1954; O'Brien 2002), but Emeljanov (1999) resurrected the family, incorporating the issid subfamilies Tonginae and Trienopinae within it, and placed Acanaloniidae as sister or daughter taxon of Nogodinidae. The monophyly of the Cixiidae has also been challenged (Holzinger *et al.* 2001). There is no agreement between different phylogenetic relationships within Fulgoromorpha (and Fulgoroidea) based on morphological evidence (Asche 1988; Emeljanov 1990; Yang & Chang 2000), molecular evidence (Bourgoin 1997) or combined morphological, palaeontological and molecular data (Bourgoin & Campbell 2002).

Studies on the nymphs of extant Fulgoroidea have advanced considerably in the last two decades (Emeljanov 2001). Fossil nymphs, in contrast, have been little studied (Szwedo *et al*. 2004). A fossil nymph suggested to be related to Fulgoroidea is *Knezouria unicus* Jell, 1993, reported from the Late Triassic, Carnian of Dinmore, Ipswich Basin,

Queensland, Australia (Jell 1993). However, several critical characters are unclear and the placement of this taxon is inconclusive. The Lower Cretaceous fossils described below are representatives of the Fulgoroidea. There is no way of determining their morphogenetic development and they cannot be assigned to any known family, therefore a separate family and genus is erected for them.

TAXONOMY

Order Hemiptera Linnaeus, 1758
Suborder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Kirkaldy, 1907
Family **Neazoniidae** fam. n.

Type genus: *Neazonia* gen. n.

Diagnosis: In general habitus similar to some nymphs of Cixiidae and Achilidae, but distinctly flattened and more elongate. Differs from nymphs of any other Fulgoroidea in peculiar agglomeration of sensory pits on frons and abdominal tergites (arranged in rows in other Fulgoroidea) and pattern of sensory pits in groups of three or four.

Genus **Neazonia** gen. n.

Etymology: From classic Greek "*neâzon*", meaning "acting like a youth". Gender feminine.

Type species: *Neazonia tripleta* sp. n., by present designation.

Diagnosis: Body slender, somewhat elongately ovoid. Head with vertex about as long as wide; face elongate, with two submedian carinae, converging at fronto-clypeal suture. Rostrum elongate, extending beyond apex of pygofer. Two rosette-like groups of sensory pits on frons, not arranged in rows. Sensory pits on thorax and abdominal tergites not arranged in rows, but rosette-like. Prothoracic tibia quadrangular in cross section, with rows of short setae along margins. Mesothoracic tibia subquadrangular in cross section. Metathoracic tibia round in cross section with apical row of teeth, but lacking lateral spine; basitarsus distinctly elongate, with apical row of teeth. Second metathoracic tarsomere of last instar short, with row of apical spines bearing subapical setae. Pygofer with distinct median fissure ventrally.

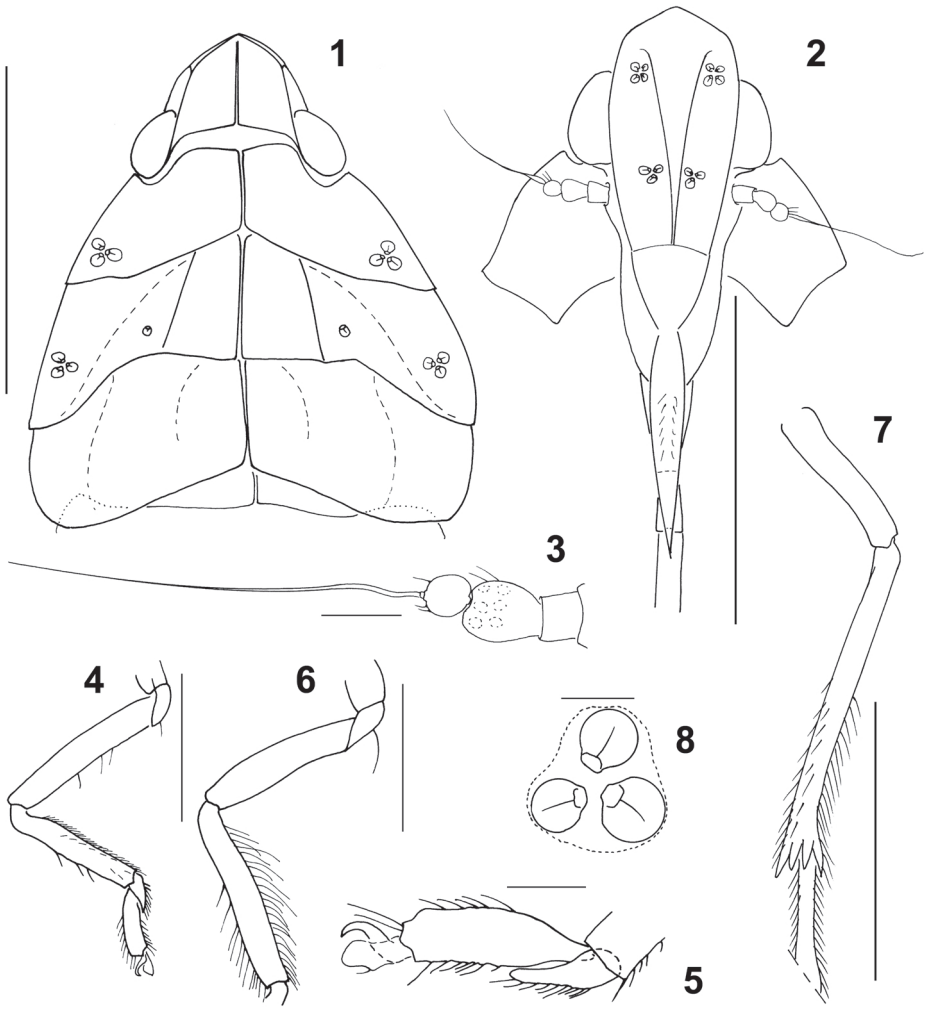
Species included: *N. tripleta* sp. n., *N. immatura* sp. n., *N. imprinta* sp. n.

Neazonia tripleta sp. n.

Figs 1–11, 24, 25

Etymology: Specific epithet refers to triplets of sensory pits on thoracic wing-pads and abdominal tergites.

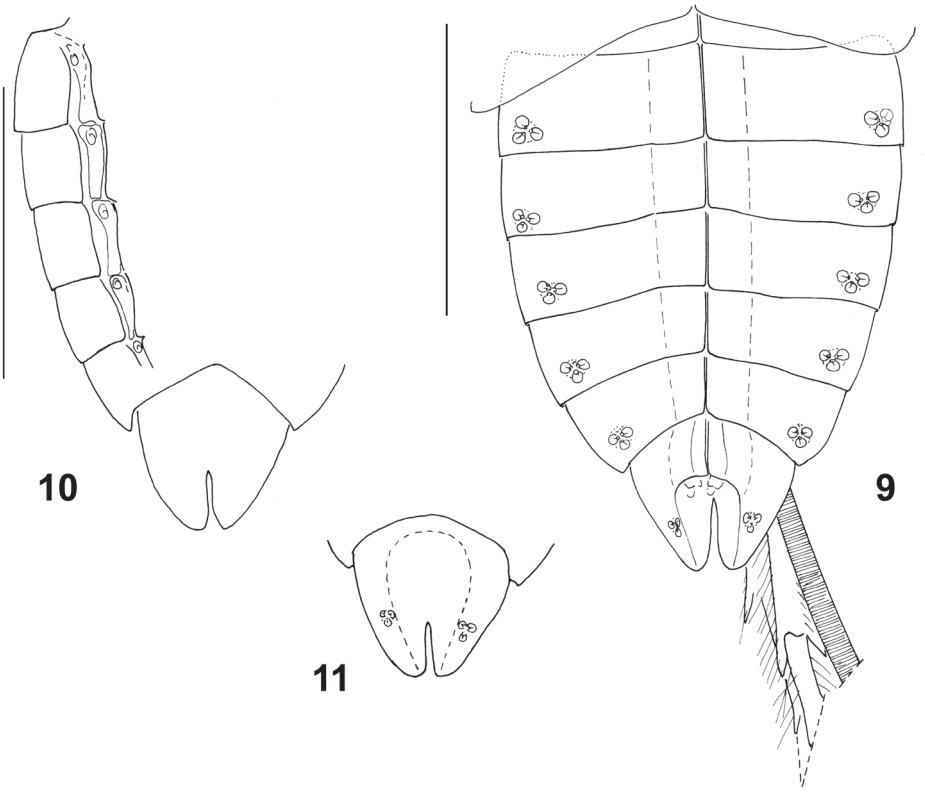
Diagnosis: More flattened dorso-ventrally than *N. imprinta*, not as elongate as *N. immatura*. Pronotum with group of three sensory pits at posterior angle (quadruplet and pentaplet near mid-line and another quadruplet at posterior angle present in *N. imprinta*). Anterior margin of pronotum distinctly incised (not incised in *N. imprinta* and *N. immatura*).



Figs 1–8. *Neazonia tripleta* sp. n.: (1) Anterior portion of body; (2) Face; (3) Antenna; (4) Right fore leg; (5) Right fore tarsus; (6) Right mid leg; (7) Left hind leg; (8) Set of sensory pits of abdominal segment. Scale bars: Figs 1, 2, 7 = 1 mm; Figs 4, 6 = 0.5 mm; Figs 3, 5 = 0.1 mm; Fig. 8 = 0.05 mm.

Description: Total length of body 3.3 mm. General shape ovoid, strongly flattened, with tip of rostrum distinctly exceeding apex of abdomen.

Head: Vertex subtriangular, a bit shorter (0.36 mm) than width at base (0.41 mm), anterior margin acutely rounded, lateral margins slightly elevated, posterior margin merely excavated posteriorly at mid-length of compound eyes, disc of vertex concave, divided by longitudinal mid-dorsal ecdysial line into left and right halves. Frons about 1.9 times as long as wide, 0.79 mm long along mid-line, 0.41 mm wide, angularly rounded at apex, broadening gradually to level of antennae, then narrowing, slightly concave at level of frontoclypeal suture. Lateral carinae originating anterior to compound eye, slightly elevated, extending to level of frontoclypeal suture; submedian carinae



Figs 9–11. *Neazonia tripleta* sp. n.: (9) Abdomen and end of body in dorsal view; (10) Ventral portion of abdomen; (11) Pygofer from below. Scale bars = 1 mm.

extending slightly below the level of bases of lateral carinae, converging medially to frontoclypeal suture and parallel to lateral carinae, disc of frons elevated in upper portion, above bases of lateral carinae, elevated between submedian carinae, concave between submedian and lateral carinae; quadruplet of sensory pits in upper portion slightly below level of bases of submedian carinae; second sensory triplet pair at level of lower margin of compound eye. Clypeus 1.00 mm long; postclypeus 0.21 mm long along mid-line, 0.46 mm long along lateral line; anteclypeus 0.70 mm long along mid-line; clypellus short, 0.09 mm long. Rostrum 3-segmented, longer than body; basal segment 0.18 mm long; subapical segment, 0.26 mm; apical segment, about 1.8 mm long (tip destroyed). Antenna 0.71 mm long; scape cylindrical, slightly shorter than pedicel; pedicel elongate subglobose, with a few sensory fields; first flagellomere globular, narrower than pedicel; arista elongate.

Thorax: Thoracic nota divided by longitudinal mid-dorsal line into three pairs of plates. Pronotum distinctly wider than head including compound eyes, anteriorly produced almost to middle of compound eyes, with distinct anteromedian lobes, anterior angles slightly protruding anteriorly, lateral margins distinctly diverging posteriorly, posterior margin weakly sinuate, posterior angle with triplet of sensory pits. Pronotum along mid-line slightly shorter (0.30 mm) than vertex along mid-line, 1.26 mm wide at posterior

angles. Mesonotum with wing pads wider (1.44 mm) than pronotum, distinctly longer (0.49 mm) than pronotum along mid-line, anterior margin arcuate anteriorly, lateral margins distinctly diverging posteriorly, posterior margin excavate, almost straight in median portion, lateral carinae present, elevated, delimiting disc of mesonotum, triplet of sensory pits present at posterior angle of wing pad, also single sensory pit visible on wing pad laterad of lateral carina. Metanotum with wing pads slightly wider (1.46 mm) than mesonotal wing pads, but shorter (0.36 mm) than mesonotum along mid-line, disc not delimited by carinae, wing pads extending to abdominal tergite 4, posterior margin excavate.

Prothoracic and mesothoracic coxae elongate, slender and ridged. Prothoracic femur slightly longer (0.59 mm) than prothoracic tibia (0.50 mm); prothoracic tibia subquadrangular in cross section, with rows of setae; first tarsomere 0.1 mm long with rows of plantar setae; second tarsomere 0.21 mm long, with rows of plantar setae and long apical setae; claws relatively large, 0.33 mm long; arolium wide, spatulate. Mesothoracic leg with femur shorter than prothoracic femur (0.56 mm), shorter than mesothoracic tibia (0.67 mm); mesothoracic tibia subquadrangular in cross section, slightly flattened with rows of long setae; mesothoracic tarsus 0.40 mm long; first tarsomere 0.14 mm long with rows of plantar setae; second tarsomere 0.28 mm long; tarsal claws distinct; arolium spatulate. Metathoracic femur 0.71 mm long; metathoracic tibia 1.20 mm long, round in cross section, with apical row of four teeth, covered with long setae; first tarsomere long.

Abdomen: 9-segmented, narrower than metathorax including wing pads, arcuately converging posteriorly, 1.82 mm long. Abdominal tergites IV to VIII with triplets of sensory pits on each side at posterior angles, delicately carinate at 1/3 laterad. Abdominal pleurites IV–VIII narrow with stigmal area in anterior portion. All abdominal sternites without median fissure. Pygofer (segment IX) triangular, 0.50 mm long along mid-line, 0.52 mm wide at base, with distinct narrow median incision ventrally, lateral lobes of pygofer with triplets of sensory pits near tip, posterior margins of pygofer lobes excavate, anal "combs" lobe-like.

Holotype: Nymph of IIIrd instar, specimen no. 1236 embedded in Canada balsam, Dany Azar coll. (Museum National d'Histoire Naturelle, Paris). LEBANON: Central Lebanon, Hammana/Mdeyrij outcrop; Lower Cretaceous, Uppermost Neocomian?–Lowermost Aptian (Azar *et al*. 2003).

Neazonia immatura sp. n.

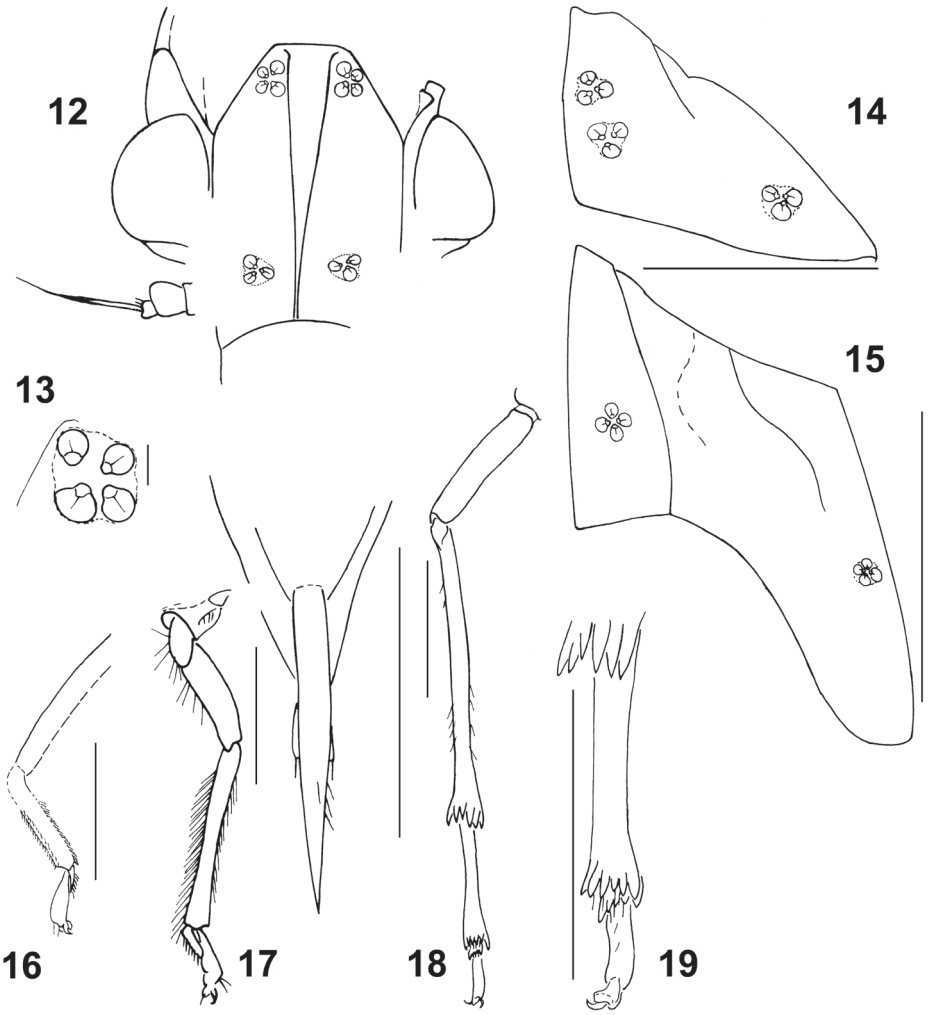
Figs 12–23, 26, 27

Etymology: Specific epithet refers to immature, nymphal stage of development of the insect preserved as inclusion in amber.

Diagnosis: More slender and elongate than *N. tripleta*, with more distinct border between thorax and abdominal segments. Anterior border of pronotum without distinct incision (distinctly incised in *N. tripleta*). Mesothoracic tibia not distinctly flattened, longer than mesothoracic femur.

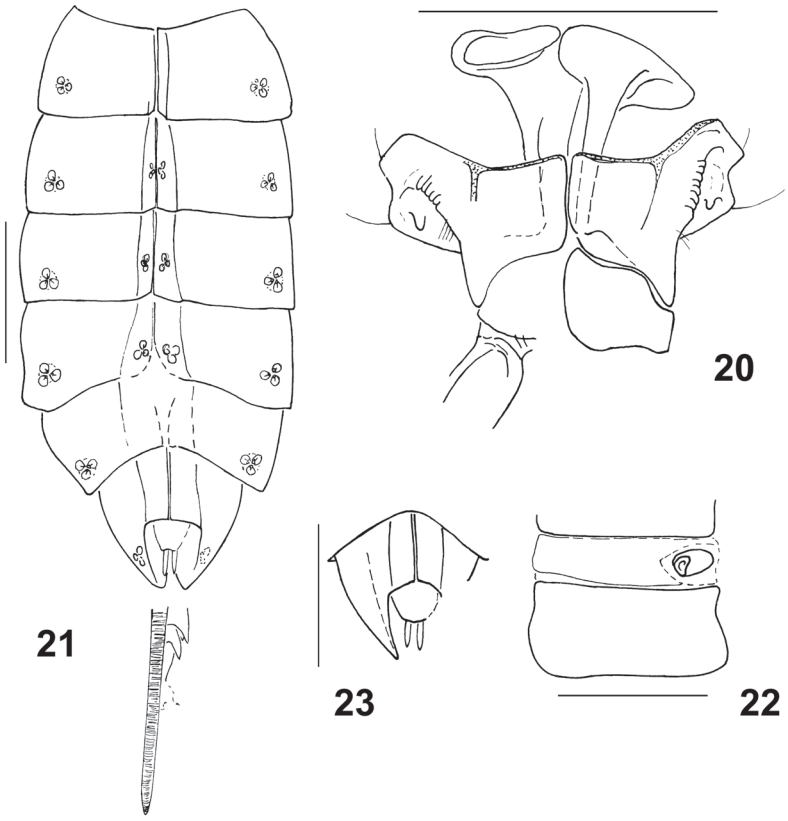
Description: Total length of body 7 mm, length with rostrum 8.5 mm. General shape ovoid, strongly flattened, with tip of rostrum extending beyond apex of abdomen.

Head: Vertex along mid-line 0.55 mm long. Frons about 1.4 times as long as wide, about 1.1 mm long along mid-line (apical portion destroyed), 0.67 mm wide, angulate



Figs 12–19. *Neazonia immatura* sp. n.: (12) Face, (13) Set of sensory pits of face, (14) Right half of prothorax, (15) Right half of mesothorax, (16) Right fore leg, (17) Left hind leg, (18) Right hind leg, (19) Right hind tarsus. Scale bars: Figs 12, 14–19 = 1 mm; Fig. 13 = 0.1 mm.

at apex, broadening gradually to level of antennae, then narrowing, slightly concave at level of frontoclypeal suture. Lateral carinae originating anterior to compound eye, slightly elevated, extending to level of frontoclypeal suture; submedian carinae extending slightly below the level of lateral carinae bases, converging medially to frontoclypeal suture and subparallel to lateral carinae, disc of frons elevated between submedian carinae, concave between submedian and lateral carinae; quadruplet of sensory pits in upper portion slightly below level of origin of submedian carinae; second sensory triplet pair at level of lower margin of compound eye. Clypeus 2.10 mm long; postclypeus 1.06 mm long along mid-line, 0.96 mm long along lateral line; anteclypeus 1.00 mm long along mid-line, clypellus short, 0.13 mm long. Rostrum 3-segmented, very long, exceeding length of body, basal segment short, subapical segment 2.37 mm, apical

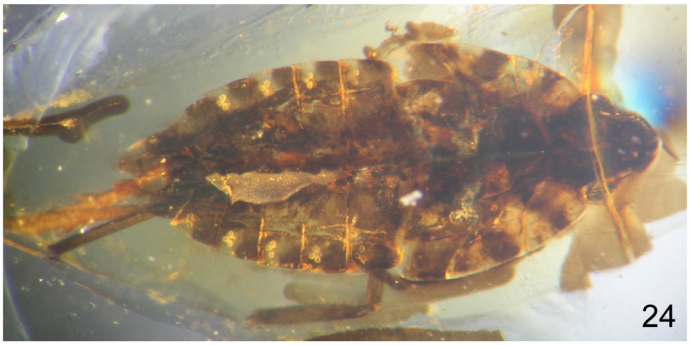


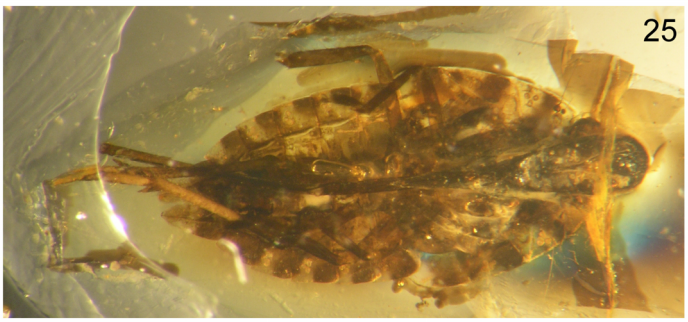
Figs 20–23. *Neazonia immatura* sp. n.: (20) Hind coxae, (21) Abdomen in dorsal view, (22) Abdominal pleural region, (23) Pygofer in dorsal view. Scale bars: Figs 20, 21, 23 = 1 mm; Fig. 22 = 0.5 mm.

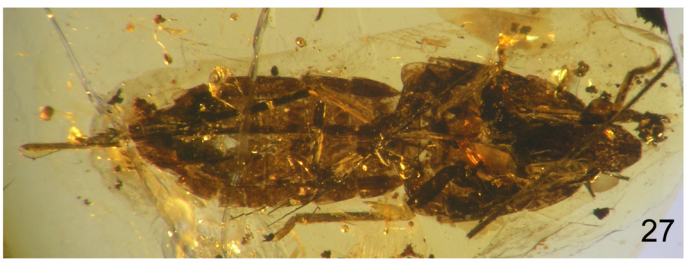
segment 3.85 mm long. Antenna about 0.92 mm long, scape cylindrical, shorter than pedicel; pedicel elongately subglobose, with a few sensory fields; first flagellomere globular, distinctly narrower than pedicel; arista long.

Thorax: Thoracic nota divided by longitudinal mid-dorsal line into three pairs of plates. Pronotum 0.65 mm long along mid-line, 1.88 mm wide, median portion of disc slightly elevated, delimited by incomplete anterior carination, anterior margin protruding between compound eyes, posterior margin excavate; pair of triplets of sensory pits present laterad of median line on disc, another triplet present at posterior angle. Mesonotum with wingpads 1.00 mm long along mid-line, 2.23 mm wide, disc elevated, delimited by lateral carinae diverging posteriad, anterior margin arcuate anteriad, lateral margins diverging posteriad, posterior margin deeply excavate; quadruplet of sensory pits present on disc slightly posteriad, another quadruplet of sensory pits present near margin of wingpad, at about half of wingpad length. Metathoracic wing pads shorter (0.75 mm) along mid-line than mesonotum, 2.08 mm wide, posterior margin shallowly excavate.

Prothoracic leg with femur as long as tibia (1 mm), prothoracic tibia subquadrangular in cross section, with rows of setae, first tarsomere 0.15 mm long with rows of plantar setae, second tarsomere 0.33 mm long, with rows of plantar setae and long apical setae,







Figs 24–27. General appearance of *Neazonia*: (24) *N. tripleta* sp. n., dorsal view; (25) *N. tripleta* sp. n., ventral view; (26) *N. immatura* sp. n., dorsal view; (27) *N. immatura* sp. n., ventral view.

claws relatively big, 0.45 mm long, arolium wide, spatulate. Mesothoracic leg with femur shorter (0.88 mm) than prothoracic femur, shorter than mesothoracic tibia (1.35 mm), mesothoracic tibia slightly flattened with rows of long setae; mesothoracic tarsus 0.5 mm long, first tarsomere 0.15 mm long with rows of plantar setae, second tarsomere 0.35 mm long, tarsal claws distinct, arolium spatulate. Metathoracic coxa with small

meracanthus, coxa ribbed near base anterior to meracanthus; metathoracic trochanter ring-like, about as long as wide; metathoracic femur 0.88 mm long; metathoracic tibia 2.18 mm long, round in cross section, with a few thickened setae present, with apical row of 1+2+3 teeth; first tarsomere 0.8 mm long, with 6 apical teeth, subapical setae present on teeth except for external teeth; second tarsomere short, 0.3 mm long, with 5 apical teeth, subapical setae present on teeth except for external teeth; apical tarsomere 0.33 mm long; tarsal claws and arolium distinct.

Abdomen: Abdomen 4.3 mm long along mid-line, 1.8 mm wide, 9-segmented, narrower than preceding metathoracic wing-pads. Abdominal tergites IV–VIII with triplets of sensory pits at posterior angles, and with submedian triplets of sensory pits close to the median line, delicately carinate at 1/5 of distance from lateral margin to the median line of tergite. Abdominal pleurites IV–VIII narrow, with stigmal area in anterior portion. All visible abdominal sternites without median fissure. Abdominal sternites VI and VII with pairs of subquadrangular areas (waxpads?). Pygofer (segment IX) triangular, about as long as wide (0.93 mm), with posterior margin excavate dorsad, with distinct narrow median incision on ventral margin, with triplets of sensory pits near the tip on lateral lobes, and pair of two sensory pits on ventral lobes, near apical angle. Pair of finger-like processes visible, probably dorsolateral processes of sternite IX. Anal segment triangular with median carination.

Holotype: Exuvium of Vth instar nymph, specimen No. 922AB embedded in Canada balsam, Dany Azar coll. (Museum National d'Histoire Naturelle, Paris). LEBANON: Central Lebanon, Hammana/Mdeyrij outcrop; Lower Cretaceous, Uppermost Neocomian?–Lowermost Aptian (Azar *et al*. 2003).

Neazonia imprinta sp. n.

Figs 28–31

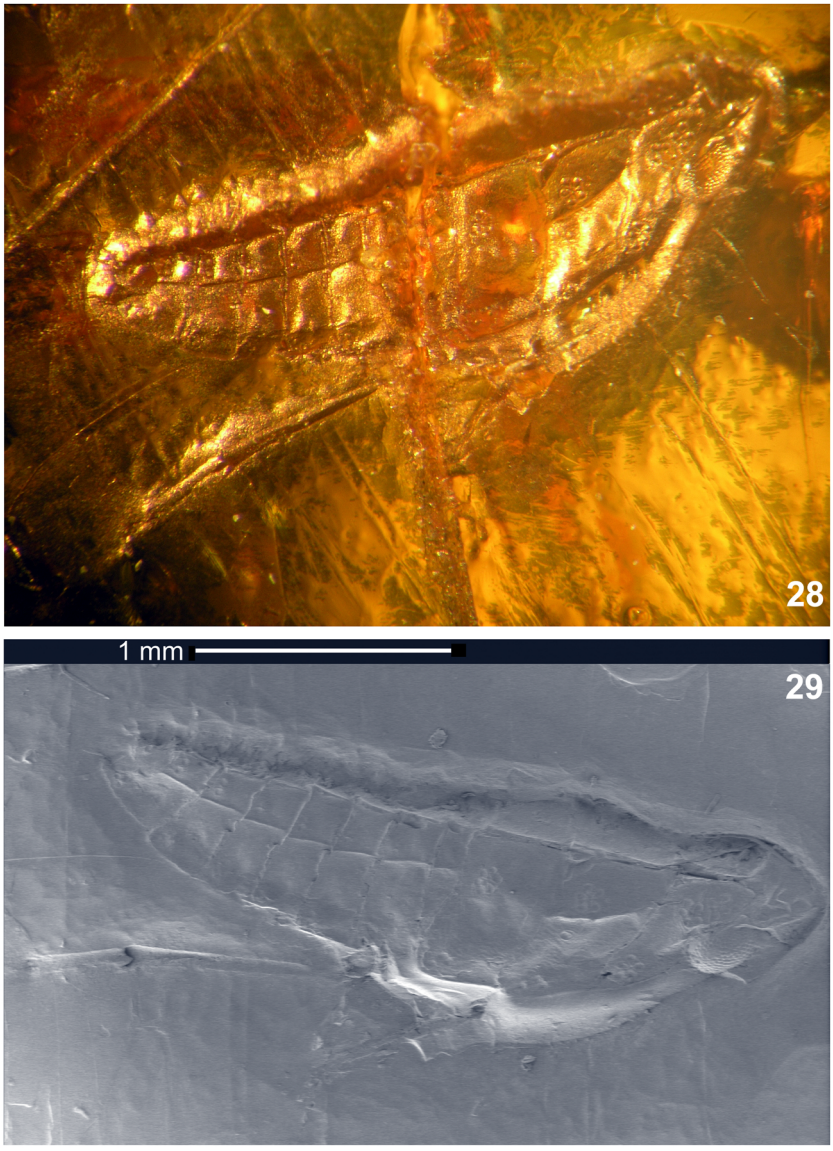
Etymology: Specific epithet refers to the state of preservation of the specimen.

Diagnosis: Less flattened than *N. tripleta* and slightly smaller. Pronotum with anterior margin not distinctly incised (incision distinct in *N. tripleta*). Quadruplet and pentaplet of sensory pits near mid-line and pentaplet of sensory pits at posterior angle of pronotum (triplet of sensory pits on posterior angle of pronotum in *N. tripleta*).

Description: Total length about 3 mm. General shape ovoid, not strongly flattened dorso-ventrally, with tip of rostrum distinctly exceeding apex of abdomen.

Head: Vertex along mid-line 0.28 mm long. Frons with quadruplet of sensory pits in upper portion. Thoracic nota divided by longitudinal mid-dorsal line into three pairs of plates. Pronotum longer (0.35 mm) than vertex along mid-line, with median portion of disc protruding anteriad; anterior angle near median line with quadruplet of sensory pits, pentaplet of sensory pits slightly posterolaterad, another pentaplet of sensory pits at posterior angle of pronotum. Mesonotum with wing pads 0.43 mm long along mid-line, about 1 mm wide, with lateral carinae delimiting disc, pentaplet of sensory pits on disc close to lateral carina. Metathoracic wing pads shorter (0.38 mm) along mid-line than mesonotum, about 1 mm wide, posterior margin shallowly excavate. Hexaplet of sensory pits on disc close to lateral carina.

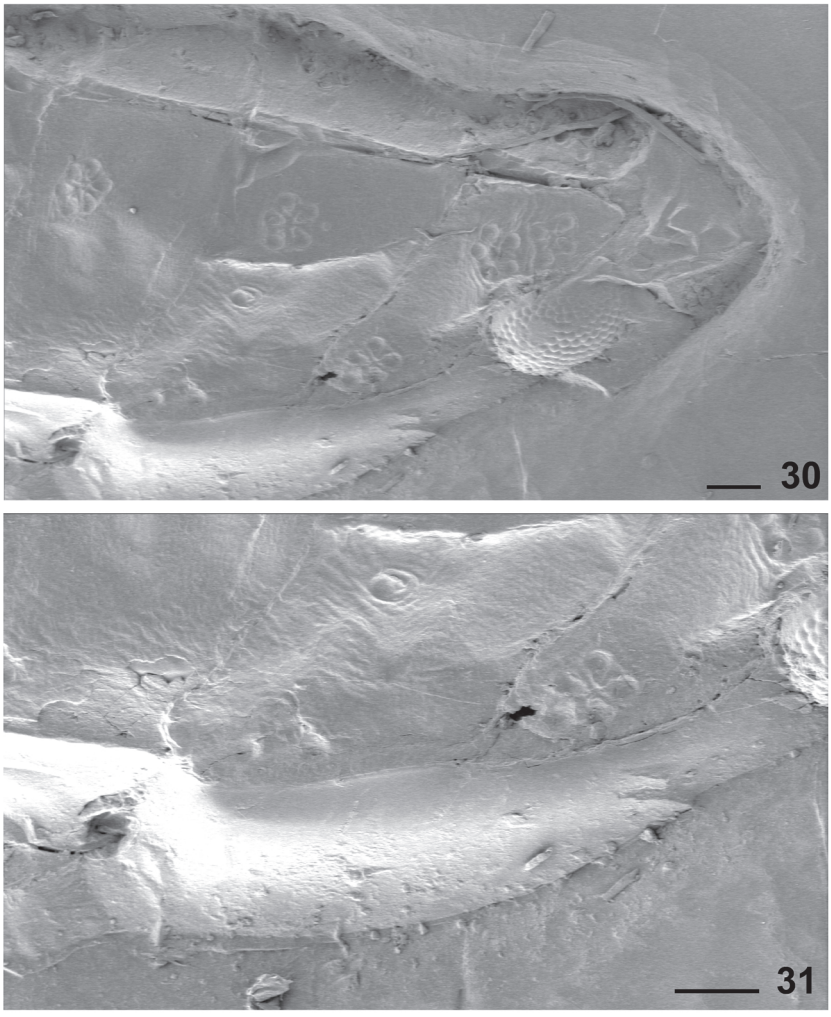
Metathoracic tibia about 1.2 mm long, with four apical teeth, probably bearing subapical setae; hind tarsus 0.6 mm long; first tarsomere 0.43 mm long with four apical teeth; second tarsomere 0.26 mm long with distinct tarsal claws and arolium.



Figs 28–29. General appearance of *Neazonia imprinta* sp. n.: (28) lateral view, light microscopy; (29) lateral view, SEM (courtesy Dany Azar).

Abdomen 1.5 mm long, abdominal tergites IV–VIII with submedian carinations at about 1/3 width laterad, with doublets of sensory pits at posterior margin mediad of carination and triplets of sensory pits at posterior angles. Pygofer apparently triangular, 0.39 mm long, with doublets of sensory pits mediad of carination at posterior margin and triplet of sensory pits at posterior angle.

Holotype: Cast of IIIrd (?) instar nymph exuvium in amber, specimen No. JG 85/7 BM 778, Aftim Acra coll. (Museum National d'Histoire Naturelle, Paris). LEBANON: Southern Lebanon, Jouar es-Souss, Jezzine outcrop; Lower Cretaceous, Valanginian–Hauterivian (Azar *et al*. 2003).



Figs 30–31. SEM of *Neazonia imprinta* sp. n. (courtesy Dany Azar): (30) anterior part of body; (31) details of thorax. Scale bars = 100 μm.

DISCUSSION

The phylogenetic relationships of the Fulgoroidea have been mainly based on characters of adults. Nymphal characters and their ontogenic development have been discussed by Emeljanov (2001), but without any proposed phylogenetic scheme. A preliminary scheme of relationships among recent Fulgoroidea based on nymphal features was proposed by Yang and Fang (1993). Nymphs of extinct Fulgoroidea have been described infrequently (Fennah 1963; Szwedo *et al*. 2004), and those that have been mentioned are limited to Eocene Baltic amber and Oligocene/Miocene Mexican amber. Recently, nymphs similar in general habitus to the species described above, but coming from Burmese amber of Albian age, have been illustrated by Grimaldi *et al*. (2002). Fulgoroidea nymphs similar to the taxa described above also occur in French amber from Archingeay of Albian age (Perrichot 2004).

The head capsules of the neazoniid nymphs described above resemble those of known achilid nymphs (Linnavuori 1951; Wilson 1983; Yang & Yeh 1994). The neazoniids differ from extant achilids by the elevated median portion of the frons, which is delimited by two carinae converging at the level of the frontoclypeal suture. Such carinae are present in an unidentified achilid nymph, described by Yang and Yeh (1994: 35–37, fig. 3A–I; Achilidae sp. 7), but these carinae diverge ventrad to the frontoclypeal suture. Submedian carinae are also present in nymphs of the genus *Cixidia* Fieber, 1866, but these carinae converge ventrally and are not fused. Submedian carinae are present in nymphs of various Derbidae (Yang & Yeh 1994), but these carinae diverge ventrally and do not converge nor are fused at the level of the frontoclypeal suture, as in the fossils described above. Submedian carinae are also present in nymphs of Delphacidae (Yang & Yeh 1994; Emeljanov 1995). These carinae are usually subparallel and do not converge nor are fused at the level of the frontoclypeal suture. If the submedian carinae are fused, as in some Delphacidae, they are unlikely to be homologous to the median carina of higher Fulgoroidea (Emeljanov 1995). These features suggest Neazoniidae should be placed close to the base of the common stock of recent Fulgoroidea, and that the fusion of the submedian carinae at the level of the frontoclypeal suture could be considered as a basal condition, and should be found in nymphs of Jurassic Fulgoridiidae.

The structure of the antenna in neazoniid nymphs seems to be very similar to that of nymphs of extant Fulgoroidea. The origin of the polymerised flagellum of Fulgoroidea is still unclear (Yang & Hsieh 1994). Emeljanov (1987) postulated that the polymerised flagellum of Fulgoroidea is a result of imaginalization of the larval antennae, while Yang & Hsieh (1994) proposed that the polymerised flagellum is derived from the filiform flagellum.

An exceptional feature of the fossil nymphs is the extremely long rostrum, which exceeds the length of the body. Such long rostra are known in adults of fossil Achilidae from Eocene Baltic amber. However, very long rostra are also known in extinct Fulgoridiidae, believed to be ancestors of the extant Fulgoroidea lineages, as well as in the poorly known genus *Knezouria* Jell from the Upper Triassic of Australia, probably representing suborder Fulgoromorpha, but with superfamilial placement not recognised. Long rostra are also known in other Mesozoic Cicadomorpha, suggesting that those insects were more often associated with woody plants, sucking sap from trunks and thick branches (Shcherbakov 2002; Shcherbakov & Popov 2002). An elongate rostrum could represent a plesiomorphic feature as it occurs in some basal fulgoroid taxa such as Neazoniidae, Cixiidae and Achilidae. On the other hand, it is also likely that a long rostrum could result from convergence, providing there is an adaptive requirement.

Sensory pits are characteristic of Fulgoroidea nymphs in all families except Tettigometridae and Hypochtonellidae (Yang & Yeh 1994). The sensory pit is a small cavity with a horizontal seta directed inwards and diverging from the cavity border, no longer than the diameter of the pit (Šulc 1928, 1929). Nymphs of extant Fulgoroidea are characterised by having two rows of sensory pits on the lateral portion of the frons (Emeljanov 2001). An ancestral condition, or general condition in Fulgoroidea as suggested by Emeljanov (2001), is that the setae of sensory pits are directed to the adjoining keel. In the nymphs of Neazoniidae, the sensory pits of the frons are arranged differently. One set of four sensory pits forms a quadruplet, with setae directed adradially, from the centre outwards in the upper portion of the frons; a triplet of sensory pits with

the same configuration of setae occurs in the lower portion of the frons. According to Emeljanov (2001) the ancestral arrangement of the pits on the thorax and abdomen was probably uniform, but it became strongly and differently modified on the prothorax, pterothorax, and abdomen. Emeljanov (2001) proposed the groundplan for the distribution of sensory pits in Fulgoroidea. His proposal is that sensory pits were originally arranged in longitudinal rows, with setae directed mediad or laterad. The sensory pits on the thoracic segments in Neazoniidae are grouped in sets of three, four, five or six. The sets of sensory pits are located on the discal and lateral (pectoral) areas of the pronotum, on the discal area and at the posterior angle of the mesothoracic wingpad, and on the discal area and posterior angle of the metathoracic wingpad. The arrangement of sensory pits in groups seems to be derived with respect to conditions present in the nymphs of the extant families of Fulgoroidea. It seems probable that the position of the sensory pits in Neazoniidae is also a derived condition. In the "basal" families Cixiidae and Achilidae, the thoracic sensory pits are also rearranged with respect to the theoretical model (Emeljanov 2001). Paired sensory pits are visible only on the median part of the abdominal tergites in *N. imprinta* sp. n. Sensory pits arranged in sets are present also on the abdominal tergites, including segment IX. The shape of the sensory pits on the head, thorax and abdomen, including the pygofer, differs from that in extant nymphs. The sensory pits in Neazoniidae are pear-shaped with the base of the sensory seta narrower, whereas in extant families of Fulgoroidea pits are circular with a complete raised border, or with an incomplete raised border in the shape of a horseshoe as in Derbidae, Meenoplidae, Delphacidae and probably also Cixiidae, or divided into many segments as in Flatidae (Emeljanov 2001). Various arrangements of the sensory pits probably appeared during the diversification of Fulgoroidea in the Late Jurassic and Early Cretaceous. In order to determine which arrangement represents the plesiomorphic condition and which represent apomorphic conditions, more fossil nymphs must be examined. In *Knezouria unicus* Jell, 1993 from the Upper Triassic of Australia there are "paired areas of small tubercles" associated with a sensory hair on each abdominal segment (Jell 1993). Unfortunately no trace of such structures on the face is preserved in *Knezouria*.

The apical abdominal segment in Neazoniidae is huge, slightly longer than the preceding segment, and triangular, with the pygofer lobes extended posteriad. The median fissure between the elongated lobes of sternite IX and the presence of elongate finger-like processes, probably dorsolateral processes of sternite IX, seem to represent another important feature of Neazoniidae. Similar elongate processes in nymphs of Fulgoridae are interpreted as homologues of the gonapophysis IX (Emeljanov 1994). This suggests that in these early Fulgoroidea, the female ovipositor was not strongly reduced as in some extant families. This statement is also supported by presence of a relatively elongate ovipositor (with respect to ovipositors found in extant Achilidae) in *Niryasaburnia burmitina* (Cockerell, 1917) from Albian Burmese amber (Szwedo 2004).

Abdominal tergites VI–VIII in Neazoniidae did not bear wax-exuding areas (waxpads), which are present in extant nymphs of various families (Yang & Yeh 1994; O'Brien 1991). A pair of structures resembling waxpads is present on abdominal sternites VI and VII in *N. immatura* sp. n. Externally, these pads are similar in general structure to wax gland plates known on achilid tergites (Liang & O'Brien 2002), but the question as to whether or not these structures are really waxpads remains unanswered.

The legs of neazoniid nymphs do not differ significantly from the legs of various extant Fulgoroidea nymphs. The prothoracic tibiae are quadrangular in cross section, with rows of short setae along the margins. The mesothoracic tibiae in the fossils are also subquadrangular, with rows of setae. In *N. tripleta* sp. n., the internal row is composed of very long and dense setae. The metathoracic coxae in the fossils seem to be very similar to these structures in extant families such as Achilidae, with small meracantha, but the ribbed portion present in the fossils has not been found in extant nymphs. The metathoracic trochanters seem not to differ between the nymphs of extant families and Neazoniidae.

An interesting feature of *N. immatura* sp. n. is the presence of subapical setae on the internal teeth of the apical rows of the metathoracic first and second tarsomeres, and the fact that the second tarsomere is very short in comparison to the first tarsomere. Emeljanov (1982) proposed that the absence of subapical setae on the first and second tarsomeres of the metathoracic leg should be regarded as a plesiomorphic condition within Fulgoroidea. In contrast, Van Stalle (1986) postulated that the chaetotaxy of the metathoracic tarsomeres with a double row of a variable number of teeth and setae was a plesiomorphic condition. Later, Emeljanov (1987) stated that metathoracic first and second tarsomeres with subapical setae is a plesiomorphic feature within Fulgoroidea. This supposition is supported by the presence of subapical setae in the extinct family Lalacidae from the Lower Cretaceous (Aptian) of Brazil (Hamilton 1990). This condition is also found in families regarded as phylogenetically basal: Cixiidae (some Pentastirini), Dictyopharidae and Fulgoridae (Aluntini and Aphaenini) (Emeljanov 1971, 1979, 1982). The function of the fulgoroid tarsomere macrochaetae has not been investigated. It was postulated that the subapical setae serve to detect vibrations (Dlabola 1988), since Fulgoroidea communicate via substrate-borne vibrations (Howarth *et al*. 1990; Tishechkin 1997, 1998, 2003).

Studies on nymphs, particularly the last instar, of extant Fulgoroidea have advanced considerably in the last two decades (Emeljanov 2001). In contrast, fossil nymphs have been poorly studied. It has been assumed that until the mid-Cretaceous most fulgoroid nymphs dwelled in the soil or were cryptic on their host plants (Shcherbakov 2002; Shcherbakov & Popov 2002). Shcherbakov (2002) and Shcherbakov and Popov (2002) postulated that achilids were the first fulgoroids with mycetophagous nymphs, as are Cixiidae and Derbidae, which, with Achilidae, form a monophyletic entity based on nymphal features (Yang & Yeh 1994). Particular types of mutualistic relationships between plant roots and fungi (e.g. ectomycorrhizal, ericoid and orchid mycorrhizas) originated in the Jurassic or Cretaceous and evolved during the period of rapid angiosperm radiation in the Cretaceous (Brundrett 2002). Sorensen *et al.* (1995) suggested that early Fulgoromorpha initially evolved to feed on roots and fungal hyphae, which existed in subterranean/semisubterranean (duff) niches, much as many of their immatures do now (Wilson *et al.* 1994). All of those assumptions are supported by the nymphal morphological features of fossil Neazoniidae described above. A cryptic, flattened shape and long rostrum suggests that these nymphs could live under bark or in cavities and the presence of debris particles in a piece of amber further supports the proposed feeding association. The Neazoniidae may have lived in gymnosperm forests, which diversified during the Late Jurassic and Early Cretaceous (Taylor 1988). The Neazoniidae, Lalacidae and some undescribed fossils could be representatives of the period of intense faunistic

reorganisation of insect assemblages, the "mid-Cretaceous biocoenotic crisis" (Rasnitsyn 1988; Zherikhin 1978, 1993, 2002). The mid-Cretaceous appearance and disappearance of families in the fossil record, or faunistic turnover, is clearly demonstrated by palaeoentomological data. This record may be interpreted as an endogenous community crisis evoked by competitive replacements in the early successional vegetation (Zherikhin 1993, 2002). Drastic vegetational changes in mid-Cretaceous times, during which the gymnosperm- and fern-dominated flora were replaced by angiosperm-dominated communities, was of greater importance in insect history than the Mesozoic/Cainozoic boundary with its famous dinosaur extinction.

The exact placement of Neazoniidae in a phylogeny scheme of Fulgoroidea and Fulgoromorpha remains unresolved. The results of preliminary analysis suggest that this family is near the basal lineage of extant Fulgoroidea–Cixiidae–Delphacidae and Achilidae (+Achilixiidae)–Derbidae lineages.

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A new hangingfly (Insecta: Mecoptera: Bittacidae) from the Middle Jurassic of Inner Mongolia, China

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ABSTRACT

A new genus of Bittacidae, *Mongolbittacus* gen. n., based on *Mongolbittacus daohugouensis* sp. n., is described from the Middle Jurassic of Inner Mongolia, China. The presence of a four-winged specimen enables documentation of the intraspecimen variation of wing venation. *Mongolbittacus* appears to be related to the genera *Orobittacus*, *Microbittacus*, *Mesobittacus*, *Preanabittacus*, *Anabittacus*, *Baissobittacus*, *Liaobittacus*, *Jichoristella* and *Antiquanabittacus* because of the presence of three synapomorphies, i.e. MP4+CuA1+2 simple; *Kreuz der Bittaciden* (rp3+4 + ma–mp1+2 and mp1+2–mp3 crossveins) not aligned; and crossvein c–sp absent.

KEY WORDS: Mecoptera, Bittacidae, hangingflies, Jurassic, China, new taxa, wing venation.

INTRODUCTION

Bittacidae is a small family of insects, but a major family of mecopterans, with more than half of its genera known from the Mesozoic (Handlirsch 1939; Sukatsheva 1990; Novokschonov 1993, 1997*a*, *b*; Ren 1993, 1997; Zhang 1993; Ansorge 1996; Petrulevičius & Martins-Neto 2001; Petrulevičius & Jarzembowski 2004). Cenozoic records are scarce and in most cases are assigned to extant genera (Jarzembowski 1980; Novokschonov 1993; Petrulevičius 1998, 1999, 2001, 2003).

Living bittacids are widespread in both temperate and tropical climates. Their wings are distinctly elongate and slender in their basal third. They are called hangingflies because they often hang by their fore legs or fore and middle legs from branches within low vegetation. They are predacious, being able to catch up to five insects at a time (Londt, review comment). Hangingflies usually occur in mesic habitats, including stream margins; slowly flying short distances and occasionally extracting nectar from blossoms. Larvae are terrestrial and detritivorous (Byers 1991).

MATERIAL

Mecoptera, particularly Bittacidae, are numerous in the Jurassic–Cretaceous of China. The material described herein was found by one of the authors (DYH), at Daohugou, Ningcheng County, Inner Mongolia, China, in the Jiulongshan Formation, Middle Jurassic (Aalenian–Bajocian) age. The specimen is a bi-dimensional impression. The matrix is a well cemented calcareous grey siltstone. The fossil is in association with

valves of Conchostraca. The material has been deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing (NIGPAS).

TAXONOMY

In the present study, we use the wing-venation nomenclature of Kukalová-Peck (1983, 1991) and the phylogenetic classification of Bittacidae proposed by Novokschonov (1993). For discussion regarding the recent phylogenetic classifications of Bechly and Schweigert (2000) and Ansorge (1996), see Petrulevičius and Jarzembowski (2004).

Order Mecoptera Packard, 1886
Infraorder Raptipedia Willmann, 1987
Family Bittacidae Handlirsch, 1906
Genus **Mongolbittacus** gen. n.

Etymology: From the locality of origin of the specimen.

Type species: *Mongolbittacus daohugoensis* sp. n., by present designation.

Diagnosis: The main venational characters of the genus are as follows: (1) basal part of wing narrow; (2) RP3+4 + MA plus RP3+4 distinctively curved; (3) MP4+CuA1+2 simple; (4) *Kreuz der Bittaciden* [rp3+4 + ma–mp1+2, mp1+2–mp3 crossveins] not aligned; (5) crossvein c–sp absent; (6) RA simple; (7) wide posterior anal field; (8) AA3+4 strongly curved posteriorly and linked to AP1+2 by a short crossvein.

Comparison: Characters 1 and 2 are synapomorphies of Bittacidae *sensu* Novokschonov (1993). Characters 3, 4 and 5 are synapomorphies of the new genus and *Orobittacus* Villegas and Byers, 1981, *Microbittacus* Novokschonov, 1993, *Mesobittacus* Handlirsch, 1939, *Preanabittacus* Novokschonov, 1993, *Anabittacus* Kimmins, 1929, *Antiquanabittacus* Petrulevičius & Jarzembowski, 2004, *Baissobittacus* Novokschonov, 1997, *Liaobittacus* Ren, 1993, and *Jichoristella* Ren, 1994.

Character 6 seems to be a synapomorphy of *Anabittacus*, *Mesobittacus*, *Jichoristella*, *Liaobittacus*, *Antiquanabittacus* and *Mongolbittacus* gen. n. This character was considered a symplesiomorphy by Petrulevičius and Jarzembowski (2004), but the most basal bittacid genus *Orthobittacus* has an RA bifurcated as do the rest of the genera of the family. Thus, it is more parsimonious to consider that this character is an acquisition of these genera.

Character 7 is shared by *Anabittacus*, *Jichoristella*, *Liaobittacus*, *Antiquanabittacus*, *Orobittacus* and *Mongolbittacus* gen. n.

Character 8 is shared by *Antiquanabittacus* and *Orobittacus obscurus* Villegas & Byers, 1981. This character is in conflict with two synapomorphies which strongly support the group formed by *Antiquanabittacus*, *Anabittacus* and *Jichoristella* i.e. RP bifurcating more basally than MP1+2, and MP3 + MP4 + CuA1+2 short (Petrulevičius & Jarzembowski 2004).

Discussion: The genera *Orthobittacus* Willmann, 1989 and *Plessiobittacus* Novokschonov, 1997 are readily distinguished from the new genus by their supernumerary MP veins. The absence in the new genus of the apomorphic state RA3+4, which is convex posteriorly, separates it from the fossil genera *Asiobittacus* Novokshonov, 1993, *Scharabittacus* Novokshonov, 1993, *Probittacus* Martynov, 1927, *Sibirobittacus*

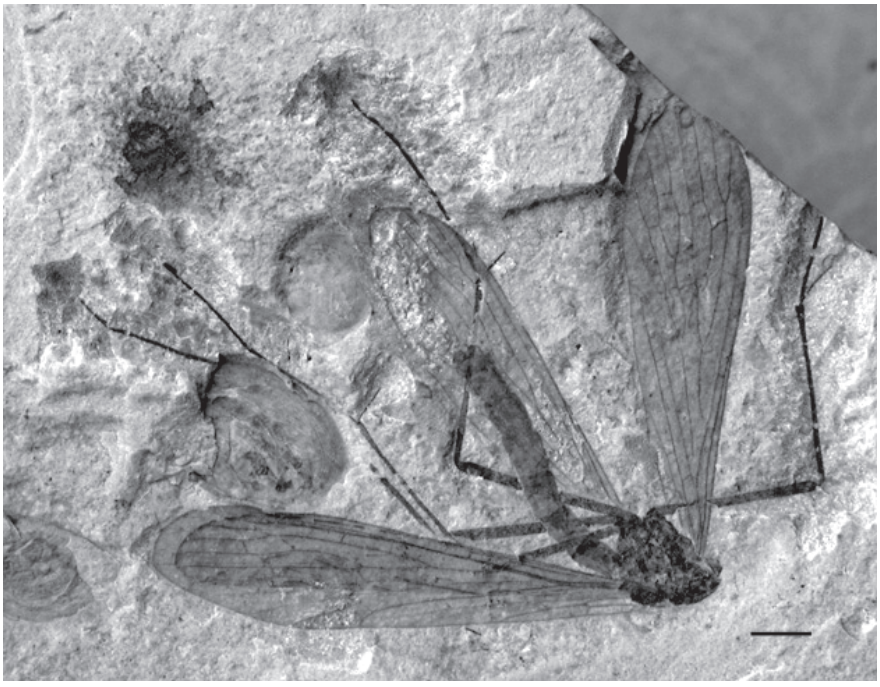

Fig. 1. *Mongolbittacus daohugouensis* gen. et sp. n., holotype. Scale bar = 2 mm.

Sukatcheva, 1990, *Telobittacus* Zhang, 1993, *Megabittacus* Ren, 1997, *Cretobittacus* Novokshonov, 1993, *Prohylobittacus* Novokshonov, 1993, *Palaeobittacus* Carpenter, 1928, and all recent genera except *Orobittacus* and *Anabittacus*. *Mongolbittacus* gen. n. is included in a possibly monophyletic group formed by *Orobittacus*, *Microbittacus*, *Mesobittacus*, *Preanabittacus*, *Anabittacus*, *Baissobittacus*, *Liaobittacus*, *Jichoristella* and *Antiquanabittacus*. In these genera, MP4+CuA is simple, *Kreuz der Bittaciden* is not aligned, and the crossvein c–sp is absent. *Orobittacus* and *Jichoristella* differ from *Mongolbittacus* gen. n. in that their RP1+2 is simple.

Simple RA is shared by *Anabittacus*, *Antiquanabittacus* (Petrulevičius & Jarzembowski 2004), *Jichoristella*, *Liaobittacus*, *Mesobittacus*, and *Mongolbittacus* gen. n. A wide posterior anal field is shared by *Anabittacus*, *Antiquanabittacus*, *Jichoristella*, *Liaobittacus*, *Mongolbittacus* gen. n. and *Orobittacus*. The last two characters are in conflict as *Orobittacus obscurus* has a bifurcated RA and *Mesobittacus* has a normal development of the posterior anal field. *Orobittacus* can be excluded for placement of the new species since it has a simple RP1+2. *Jichoristella*, *Anabittacus* and *Antiquanabittacus* can be excluded since RP bifurcates more basally than MP1+2 and the MP3+MP4+CuA1+2 is short in these genera. *Anabittacus* is also excluded by its highly specialised wing venation with many autapomorphies, viz. strongly curved RP–RP1, and loss of a common branch MP3+4 + CuA1 (because MP4+CuA arises at the same level as MP1+MP2 (Willmann 1989, fig. 93)). *Mesobittacus* is similar to the new genus but can be excluded because it has a CuA arising from Cu at a right angle in the fore wings and has shorter anal veins.

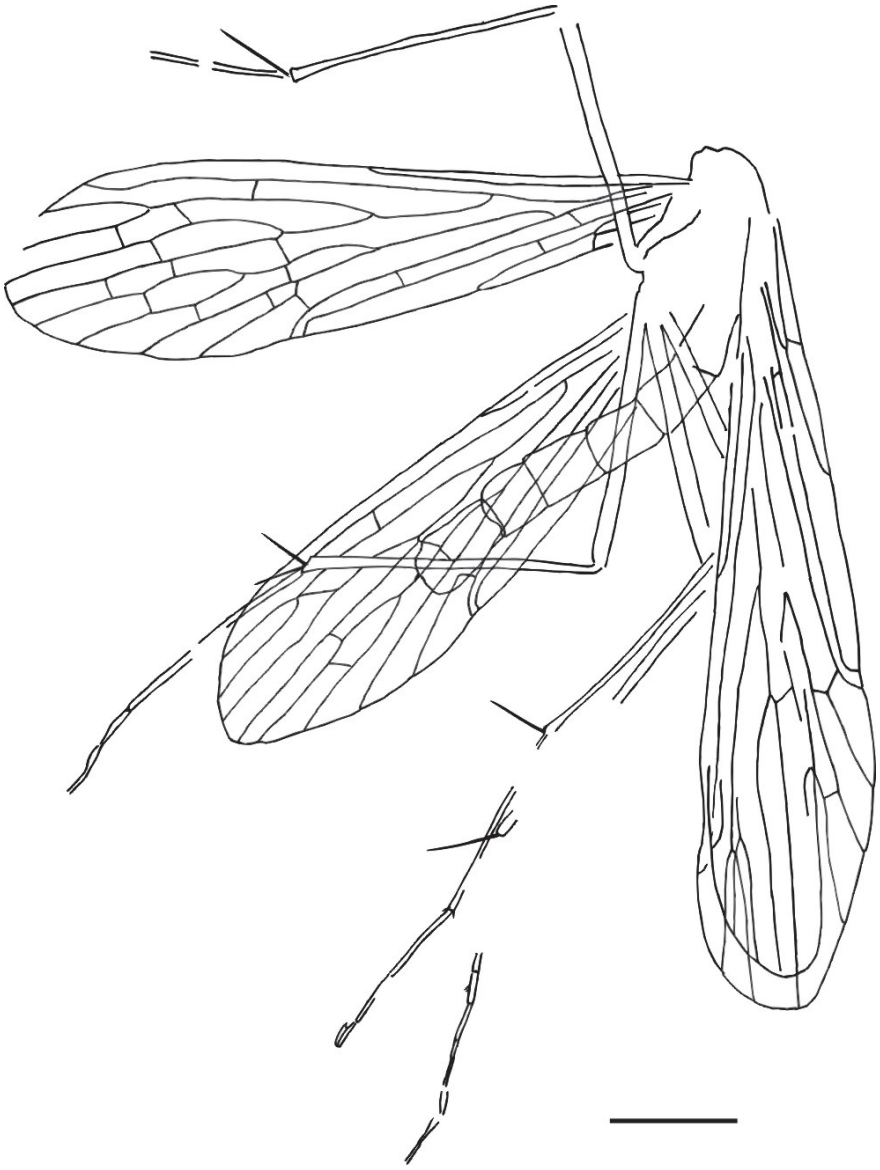

Fig. 2. *M. daohugouensis* holotype, camera lucida drawing. Scale bar = 2 mm.

Mongolbittacus shares with *Antiquanabittacus* and *Orobittacus obscurus* a strongly, posteriorly curved AA3+4 which is linked to AP1+2 by a short crossvein. However, the group formed by *Jichoristella*, *Antiquanabittacus* and *Anabittacus* seems to be well supported by two strong synapomorphies, i.e. basal shifting of the RP1+2+RP3+4+MA bifurcation, and MP3+MP4+CuA1+2 short or non-existent (Petrulevičius & Jarzembowski 2004). Therefore it is assumed that the above character is convergently similar in *Mongolbittacus*, *Antiquanabittacus* and *Orobittacus* and thus is an apomorphy of the new genus.

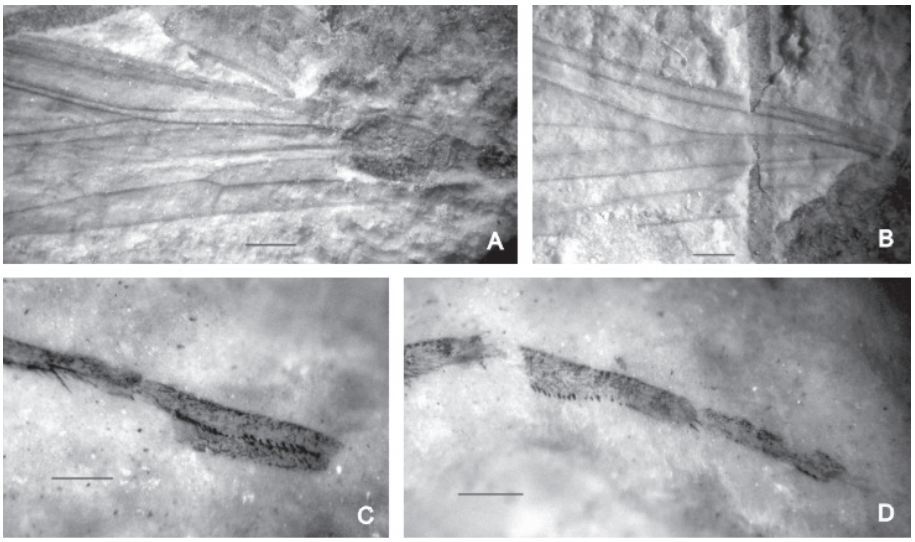

Fig. 3. *M. daohugouensis* holotype: (A) anal field of right fore wing; (B) anal field of left fore wing; (C) fore or middle last two tarsomeres; (D) hind last two tarsomeres. Scale bars = 0.2 mm.

Mongolbittacus daohugouensis sp. n.

Figs 1–4

Etymology: After type locality.

Description:

Body. Abdomen 6.5 mm long, with 7 visible segments, last segment rounded with cerci; hind and mid (?) femur about 4.1 mm long, hind tibia 4.5 mm long, mid (?) tibia 4.3 mm long, hind tarsus about 5.3 mm long, mid tarsus 6.5 mm long; two long tibial spurs on all 4 legs; tarsomere 3 of midtarsus (?) with several long hairs along ventral plane (Fig. 3C); tarsomere 4 of hind tarsus enlarged and with several strong, small ventral spines (Fig. 3D); tarsomere 5 of hind tarsus with less strong, small ventral spines; pretarsal claws not preserved.

Wings. Fore wing (basal part missing): preserved length 11.1 mm; maximum width 3.2 mm; basal part of wing narrow; ScP reaching wing margin just basal to RP fork; ScP without crossveins to RA; R continuous with RA; RA simple and slightly spoon-like, reaching antero-apical wing margin; crossvein between RA and RP1+2; sigmoidal crossvein between RP1+2 and RP3+4; crossvein between RP2 and RP3+4; crossvein between RP3+4 and MA; RP arising from R at an acute angle; RP1+2 arising at almost a right angle from RP, sub-symmetrical with RP3+4+MA; RP1 and RP2 bifurcating symmetrically; RP1+2 forking just basal to curved part of RA; MA nearly straight though fractured by anterior part of the *Kreuz*; RP3+4+MA + RP3+4 sigmoidal; RP3+4 arising from RP3+4+MA at an acute angle, bent posteriorly after crossvein to RP1+2, and running more or less parallel to MA; separation of RP3+4 basal to bifurcation of MP1+2; *Kreuz* not aligned; posterior part of *Kreuz* reaching MP3 just distal from its base; two crossveins between MA and MP1; one crossvein between MP1 and MP2; one crossvein between MP2 and MP3; MP4 fused with CuA1+2 and closely aligned

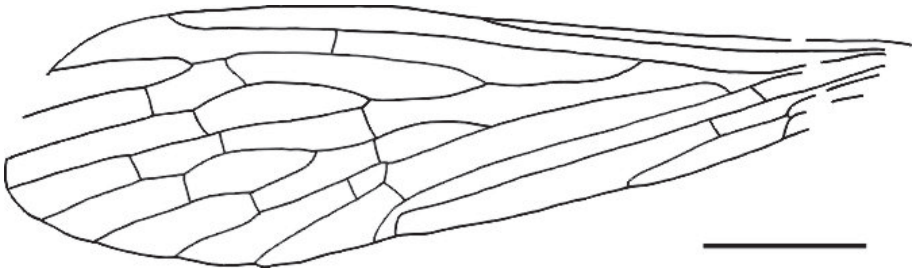

Fig. 4. *M. daohugouensis* holotype, camera lucida drawing of right fore wing. Scale bar = 2 mm.

with MP3; one crossvein between MP3 and MP4+CuA1+2; CuA arising from Cu at an oblique angle and fused with MP for a short distance; CuA3+4 and CuP running parallel to each other; final part of CuP strongly curved and reaching wing margin at approximately right angles; AA3+4 reaching wing margin slightly distal to bifurcation of R; one crossvein between CuP and AA3+4; AA3+4 strongly curved posteriorly and linked to AP1+2 by short crossvein; in left wing, curvature of AA3+4 is more pronounced and crossvein longer than in right wing, where AA3+4 is less curved (Figs 3A, 3B); AP1+2 running well separated from wing margin and reaching wing margin just basal to CuA, producing a wide posterior anal field; AP1+2 reaching wing margin with a strong curvature after crossvein to AA3+4, the curvature fractured in the left wing and rounded in the right (Figs 3A, 3B).

Hind wing (basal part missing): preserved length 9.5 mm; maximum width 2.7 mm; ScP reaching wing margin basal to forking of RP; ScP without crossveins to RA, shorter than in forewing; R continuous with RA; RA simple and slightly spoon-like (?), reaching antero-apical wing margin; crossvein between RA and RP1+2; oblique crossvein between RP3+4 and base of bifurcation of RP1 and RP2; RP arising from R at approximately right angles; RP1+2 arising from RP at an acute angle, sub-symmetrical with RP3+4 + MA; RP1 and RP2 bifurcating sub-symmetrically; MA nearly straight, fractured by anterior part of the *Kreuz*; RP3+4+MA + RP3+4 sigmoidal; RP3+4 arising from RP3+4+MA at an acute angle, bent posteriorly after crossvein to RP1+2, and running more or less parallel to MA; separation of RP3+4 basal to bifurcation of MP1+2; *Kreuz* not aligned; posterior part of *Kreuz* reaching MP3 just distal from its base (?); a single crossvein between MA and MP1 and between MP1 and MP2; MP4 fused with CuA1+2 and closely aligned with MP3; CuA3+4 and CuP running parallel to each other; final part of CuP strongly curved, reaching wing margin at a right angle.

Holotype: NIGPAS 133709, almost complete and articulated female specimen, without head; thorax not well preserved in lateral view, mid and hind legs legs preserved. CHINA: *Inner Mongolia*: Ningcheng County, Daohugou; Middle Jurassic, Jiulongshan Formation.

Remarks: Bittacidae are usually preserved disarticulated and are thus represented by isolated wings in the fossil record. The entomofauna from the Middle Jurassic of Daohugou is mainly represented by complete specimens. This introduces the possibility of observing intraspecimen variation in the wing venation. This variation was observed in *M. daohugouensis* in the venation of the anal field (Figs 3A, 3B). Variation of the wing venation in different specimens of the same recent species has been studied by different authors and summarised by Willmann (1989), who also provided new data. This variation is not documented in fossil specimens of the family, and the existence of

such variation at about 170 Ma is of great interest. We have to take into account the review comment of Dr J.G.H. Londt, stating that the specimen appears to be quite small for a bittacid and that small individuals may possess 'simplified' morphology—maybe even reduced venation. As this particular specimen is unique, being the only specimen of this species available for study, we are unable to estimate the variation in size between individuals of this species. Thus it is a possibility that the intraspecimen variation of wing venation in *M. daohugouensis* gen. et sp. n. is due to its small size. Future discoveries and subsequent studies of new specimens may help to resolve this matter.

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A revision of Eocene Bittacidae (Mecoptera) from Baltic amber, with the description of a new species

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ABSTRACT

The Bittacidae of the Eocene Baltic amber are revised, recognising one species of the genus *Bittacus*, *B. succinus* Carpenter; the remaining four species are transferred to *Hylobittacus* Byers; *H. antiquus* (Pictet) is resurrected from synonymy; one new species is described: *H. picteti* sp. n.

KEY WORDS: Baltic amber, Mecoptera, Bittacidae, *Bittacus*, *Hylobittacus*, hanging fly, Eocene, new species.

INTRODUCTION

The family Bittacidae comprises about 270 extant species, which mainly inhabit tropical and subtropical regions. The oldest known fossil representative is *Archibittacus exilis* Riek, 1955 from the Upper Triassic of Australia (Riek 1955). Their greatest known generic diversity was in the Jurassic, with ten genera currently recognised (Novokshonov 2002).

The oldest known Palaeogene record of the family is *Thyridates novokschonovi* Petrulevičius, 2003 from the late Palaeocene Maíz Gordo Formation of Argentina (Petrulevičius 2003). The Eocene records of Bittacidae include *Palaeobittacus eocenicus* Carpenter, 1928 and *Bittacus egestionis* Carpenter, 1955 from the Early Eocene Green River Formation in western USA; and the Baltic-amber species discussed here. Oligocene bittacids include *Bittacus veternus* (Cockerell, 1921) and the unnamed species *Bittacus* sp. A (Jarzembowski 1980) from the Late Eocene/Early Oligocene of the Isle of Wight in Southern England, and *Bittacus biamensis* Novokshonov 1993 from Biamo (Bol'shaya Svetlovodnaya) in Primorye, Russia (Novokshonov 1993). These are the only known fossil species of *Bittacus* and *Palaeobittacus*; fossil *Hylobittacus* is known only from the Baltic amber.

The earliest descriptions of Bittacidae from the Baltic amber were by Pictet (1854), who described *Bittacus antiquus*, and Hagen (Pictet-Baraban & Hagen 1856), who described *B. validus*, later identified as a trichopteran (Carpenter 1976). Hagen found the original drawing of the venation of *B. antiquus* by Pictet to be incorrect and published his own reconstruction (Pictet-Baraban & Hagen 1856). Carpenter revised the generic placement of this species twice (see below).

The papers by Pictet (1854), Hagen (Pictet-Baraban & Hagen 1856) and Carpenter (1931, 1954, 1976) cover all known records of Bittacidae preserved in Baltic amber; that is, about 12 specimens altogether. Not all this material is available for study at present. The oldest specimens described by Hagen and Pictet seem to be lost, but sometimes such old, seemingly lost specimens are found in museum or private collections. Such was the fate of the famous collection of Koenigsberg, re-discovered in Goettingen, what I had an opportunity to check while being there.

The purpose of this paper is to revise the Bittacidae from Baltic amber, including material described by Carpenter (op. cit.) and 18 new specimens. Ten of them were purchased from a private source and are now in the collection of the Natural History Museum of the Institute of Systematics and Evolution of Animals in Krakow. Ten additional specimens of Bittacidae were also examined, but are not listed as they remain in private collections. However, this material is included in the conclusions presented within this paper. The classification to the genera *Bittacus* and *Hylobittacus* follows Byers (1979) and is based on the presence of two pterostigmal cross-veins versus one, respectively. In applying this system, I also consider the opinion of Weitschat and Wichard (2002).

MATERIALS AND METHODS

This study was based on an examination of 28 fossils in Baltic amber kept in the following institutions: the Natural History Museum, London (BMNH); Deutsches Entomologisches Institut im Zentrum für Agrarlandschafts- und Landnutzungsforschung e.v., Müncheberg, Germany (DEIM); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); the Natural History Museum of the Institute of Systematics and Evolution of Animals, Krakow, Poland (MP); Museum of the Earth, Warsaw, Poland (MZW).

All wings are shown in standard aspect, with the apex to the right; some photographs are reversed left-right for comparison with drawings (see captions). The terminology for wing venation (Fig. 1) follows Byers (1979); the terminology for genitalia follows Webb *et al*. (1975).

TAXONOMY

Family Bittacidae Handlirsch, 1906

Genus *Bittacus* Latreille, 1805

Bittacus succinus Carpenter, 1954

Figs 2, 7A

Bittacus succinus: Carpenter 1954: 39–40, figs 3B, 4C.

Diagnosis: Provided by Carpenter (1954).

Redescription:

Male.

Forewing 17 mm long (Fig. 2B). Two pterostigmal crossveins, Pcv1, Pcv2; Sc long, ending distally far beyond fork of Rs; sc–r opposite fork of Rs, which is opposite fork of Mb; numerous additional veins in cells r3, r4, r5, r6, m1, m2, m3.

Genitalia (Figs 2C, 7A): epiandrial lobe distinctly widened about proximal 1/3, gradually tapering toward apex.

Female. Unknown.

Holotype (examined): MCZ 5204 (= old no. 5112), a fairly intact male, missing some leg parts, clearly preserved on one side, with milky covering on the other.

Remarks: Upon re-examination of the holotype, the wing venation as illustrated by Carpenter (1954, fig. 3B) is in part incorrect, and a revised drawing is provided here (Fig. 2B).

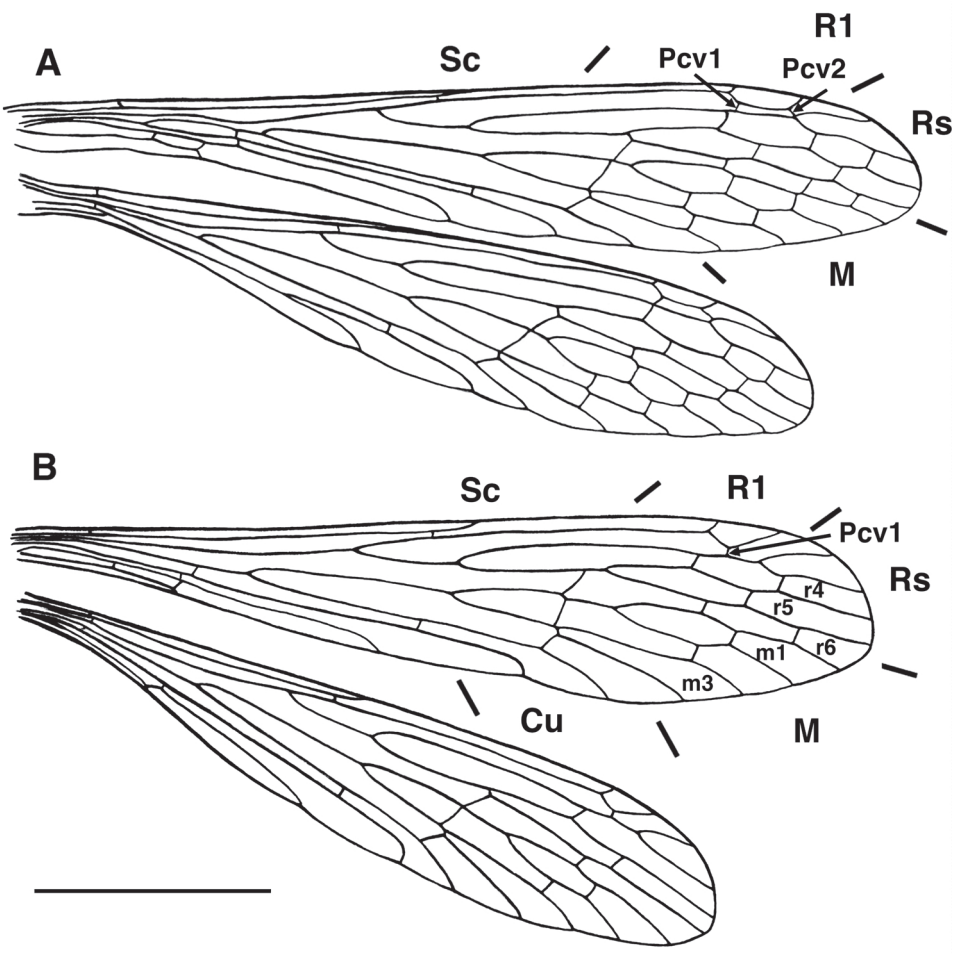

Fig. 1. Fore- and hind wing venation in extant *Bittacus* and *Hylobittacus*: (A) *Bittacus* sp., Europe; (B) *Hylobittacus apicalis* (Hagen), North America (after Byers, 1979). Abbreviations: Pcv1, Pcv2 – pterostigmal cross-veins. Scale bar = 5 mm.

Genus *Hylobittacus* Byers, 1979

Hylobittacus antiquus (Pictet, 1854), **comb. n.**

Fig. 3

Bittacus antiquus: Pictet 1854: 379, fig. 26.
Bittacus antiquus: Pictet-Baraban & Hagen 1856: 92, fig. 22.
Electrobittacus antiquus: Carpenter 1931: 410.

Diagnosis: Separated from all species of *Hylobittacus* in Baltic amber by a combination of: Sc very long, ending distally far beyond fork of Rs; additional cross-veins in cells r5, r6 and sometimes m1.

Redescription (based on female MP 1/1145/188/01):

Female.

Forewing 19 mm long, uniformly light brown, pterostigma slightly darker; shape and venation as in Figs 3D and 3E; single pterostigmal cross-vein; very long Sc reaching

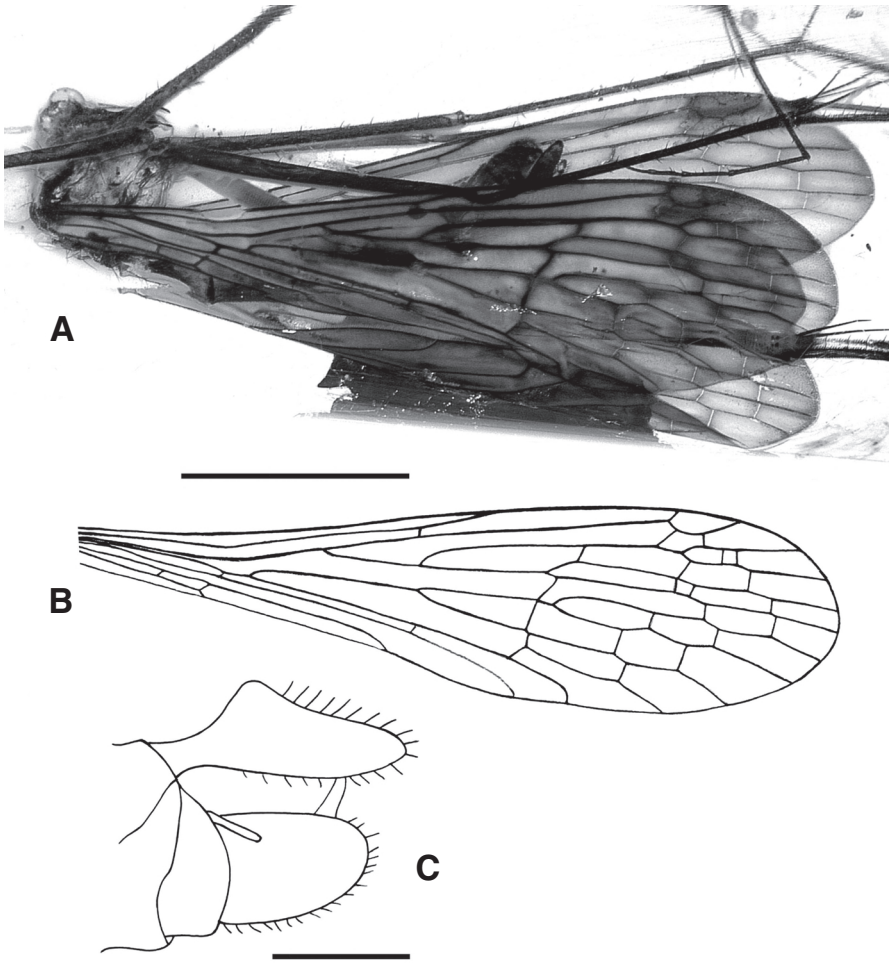

Fig. 2. *Bittacus succinus* Carpenter, holotype: (A) habitus, reversed left-right; (B) forewing; (C) male genitalia in lateral view (after Carpenter 1954). Abbreviation: e – epiandrial lobe. Scale bars: Figs 2A, 2B = 5 mm, Fig. 2C = 1 mm.

margin far beyond fork of Rs; crossvein sc–r at about nine times its length before end of Sc; 2 or 3 additional crossveins in cells r5, r6, m1.

Male. Unknown.

Material examined: MP 1/1145/188/01, female with head and thorax missing, most of the legs partially preserved, abdomen and three wings complete (donation of J. Serafin); MCZ 5210 (old number MCZ 5118), female, condition as in Carpenter (1954) determined as *B. fossilis* by Carpenter (1954).

Remarks: Carpenter reclassified this species twice. Initially, he placed it in a new, monotypic genus *Electrobittacus*, based on Pictet's (1854) drawing of the head, which he found bore an abnormally short rostrum for a bittacid (Carpenter 1931). Later, he considered this genus name to be a *nomen dubium* and, further, synonymised the species with *Bittacus fossilis*, based on a comparison of with a specimen of *H. antiquus* of his collection (female MCZ 5210 = old number 5118; Carpenter 1954) with Pictet's drawing. Carpenter also suggested that this drawing might illustrate a trichopteran. This does not

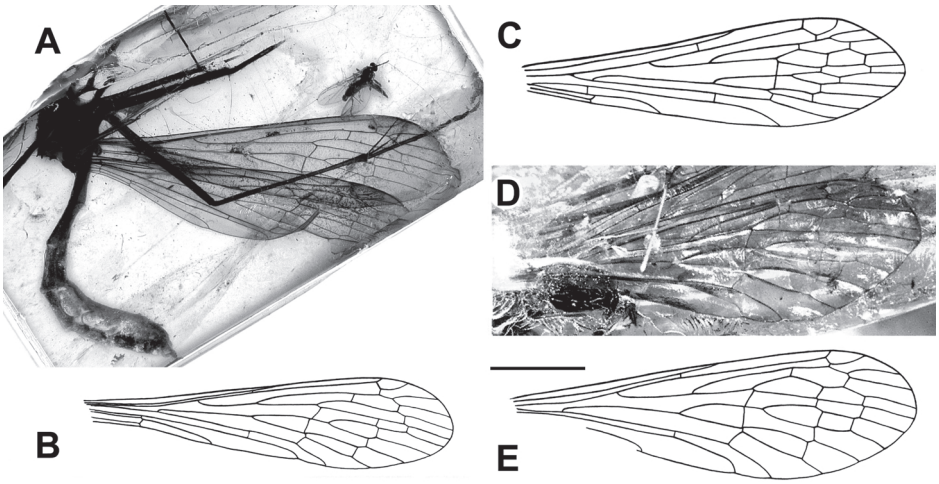

Fig. 3. *Hylobittacus antiquus* (Pictet): (A, B) specimen MZC 5210, general appearance and details of forewing venation; (C) venation of forewing (after Pictet-Baraban & Hagen, 1856); (D, E) specimen MP 1/1145/188/01, general appearance of wing and details of venation. Scale bar = 5 mm.

seem plausible, since the leg of the specimen resembles that of a bittacid and not a trichopteran.

Carpenter's procedure was incorrect for three reasons. Firstly, an improved drawing of Pictet's specimen was published by Hagen (Pictet-Baraban & Hagen 1856), who therefore should be regarded the first reviser of this species. Secondly, Carpenter incorrectly considered differences in venation in the specimen illustrated by Hagen to be non important and within the range of intraspecific variation of *B. fossilis*. And third, in his synonymy, Carpenter used a junior, instead of the senior name.

Upon examination of an additional specimen in the MP collection, the length of Sc and the presence of additional cross-veins in the apical region of the wing (Figs 3D, 3E) clearly conform to the drawing of *H. antiquus* by Hagen (Pictet-Baraban & Hagen 1856, fig. 22, table VIII; also see Fig. 3C in this paper). This is in agreement with Hagen's interpretation, and so *H. antiquus* (Pictet) is resurrected here from synonymy.

The species is now known from three specimens: the specimen which was illustrated by Hagen (Pictet-Baraban & Hagen 1856, fig. 22; Fig. 3C, this paper), a second in the MP collection (MP 1/1145/188/01, Fig. 3E), and a third examined by Carpenter and included by him in *H. fossilis* (MCZ 5210; Figs 3A, 3B). Although the location of the specimen described by Pictet and examined and illustrated by Hagen is unknown at present, a neotype is not designated here, assuming that it is not permanently lost nor destroyed.

Hylobittacus fossilis (Carpenter, 1954), **comb. n.**

Figs 4, 7B

Bittacus fossilis: Carpenter 1954: 37, 38, figs 3A, 4B.

Diagnosis: Separated from all species of *Hylobittacus* in Baltic amber by a combination of: Sc short, ending well before fork of Rs; epiandrial lobe with deeply incised margin dorsally.

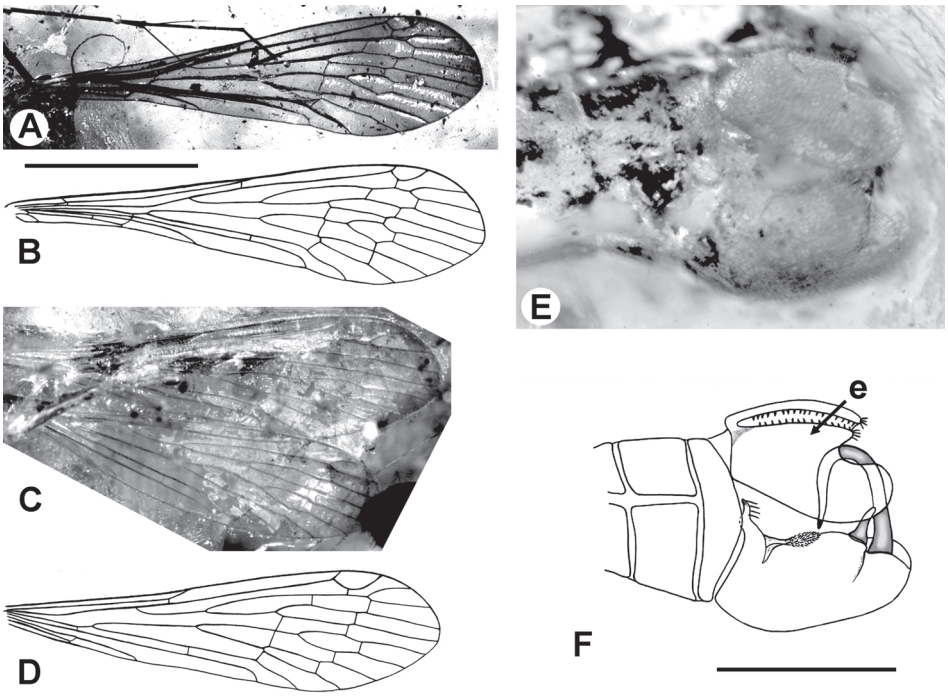

Fig. 4. *Hylobittacus fossilis* (Carpenter): (A, B) male DEIM 1150/1, general appearance of wing and details of venation; (C, D) female MP/1/1/551/05/A, general appearance of wing (reversed left-right) and details of venation; (E, F) male genitalia, DEIM 1150/1 general appearance and details. Abbreviation: e – epiandrium. Scale bars: Figs 4A–D = 5 mm, Figs 4E, 4F = 1 mm.

Redescription:

Male.

Forewing (Figs 4A–D) 13–16 mm long. Single pterostigmal cross-vein; Sc short, ending well before fork of Rs; sc–r at two to four times its length before end of Sc; cubital cross-vein below fork of Mb; no additional cross-veins in radial, medial distal cells. Genitalia (Figs 4E, 4F, 7B): epiandrial lobe with deeply incised margins dorsally, forming posterior lobe; upper, inner margin of epiandrial lobe with numerous spines; basistyle large.

Holotype (examined): MCZ 5209 (old no. 5117), male, mostly clearly preserved on one side, milky coating on portions of the other, some legs, half of right forewing and apical portion of right hind wing missing as a result of preparation.

Other material examined: MCZ 4898, specimen complete except for left wings missing, clearly preserved except for some milky covering in places; DEIM 1150/1, a complete male specimen in perfect condition (Hoffeins coll.); MP 1/1/551/05/A, female, an entire specimen in good condition, only head partially obscured; MP 1/2/552/04, three males in one piece of amber: two entire specimens in perfect condition; third one only partially preserved, without head, and only a portion of thorax and one wing present, abdomen obscured by milky layer; MP 1/1/552/04, female with only two wings, fragments of legs and abdomen preserved; MP 1/5/552/04, sex unknown, only fragments of wings and one leg preserved; MZW 19996, sex unknown, two wings and small fragment of thorax and legs preserved.

Remarks: *H. fossilis* seems to be the most frequent bittaciid found in Baltic amber (pers. observ.). Its venation shows remarkably little variation.

Fig. 5. *Hylobittacus minimus* (Carpenter): (A) holotype MCZ 5205, general appearance; (B, C) male 674/2, reconstruction of forewing and genitalia. Scale bars: Figs 5A, 5B = 5 mm, Fig. 5C = 1 mm.

Hylobittacus minimus (Carpenter, 1954), **comb. n.**

Figs 5, 7C

Bittacus minimus: Carpenter 1954: 39, fig. 4D.

Diagnosis: Separated from all species of *Hylobittacus* in Baltic amber by a combination of: Sc ending opposite fork of Rs and epiandrial lobe broad basally.

Redescription:

Forewing (based on specimen 674/2, Fig. 5B) 13 mm long; single pterostigmal cross-vein; Sc ending opposite fork of Rs; cubital cross-vein far before fork of Mb; no additional cross-veins in distal radial and medial cells.

Male genitalia (Figs 5A–C, 7C): epiandrial lobe short, without dorsal incision, broad basally; basistyle small, rather narrow.

Holotype (examined): MCZ 5205 (old no. 5113), male, condition as in Carpenter (1954).

Other material examined: DEIM 674/2, male with only two wings, fragment of thorax and abdomen partially obscured by milky cloud (Hoffeins coll.); BMNH In. 18855, entire female partially obscured by milky cloud; MP 1/3/552/04, poorly preserved female, only three wings and fragments of legs recognisable, abdomen obscured by milky cloud.

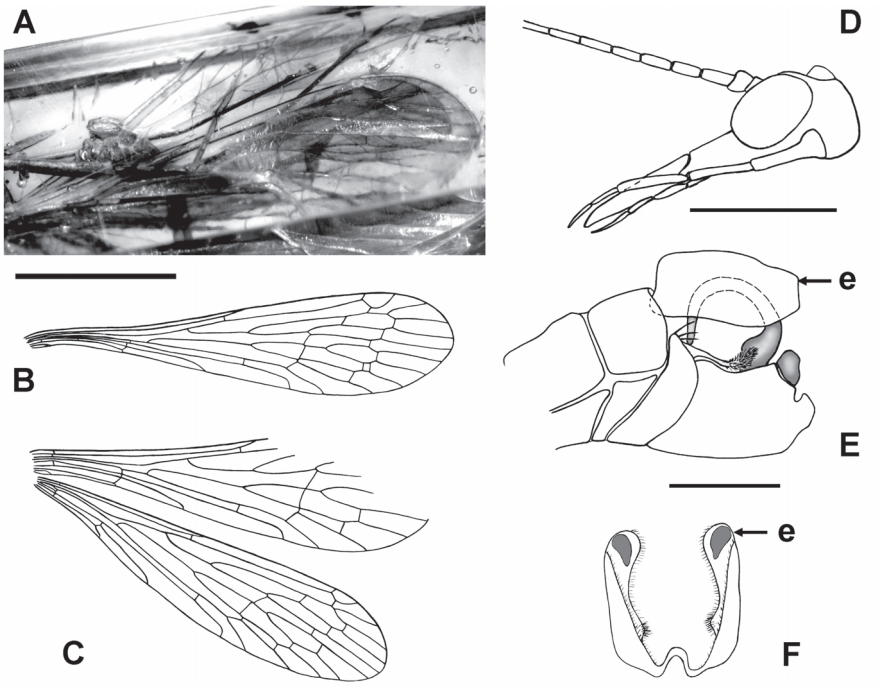

Fig. 6. *Hylobittacus picteti* sp. n.: (A, B) forewing of female 1150/2, general appearance and details of venation; (C–F) holotype DEIM 674/1: (C), fore- and hind wing, (D) head with antenna and palp, (E) male genitalia, lateral aspect; (F) epiandrium, dorsal aspect. Abbreviation: e – epiandrium. Scale bars: Figs 6A–C = 5 mm, Figs 6D–F = 1 mm.

Hylobittacus picteti sp. n.

Figs 6, 7D

Etymology: The specific epithet is a patronym formed from the surname of F.J. Pictet, author of the first description of *Bittacus* from Baltic amber over 150 years ago.

Diagnosis: Separated from all species of *Hylobittacus* in Baltic amber by a combination of: Sc ending just behind fork of Rs, epiandrial lobe broad and slightly narrowed apically, basistylus broad and large.

Description: Antenna most likely 16-segmented; palp 5-segmented (Fig. 6D).

Forewing (Figs 6A–C) 15–17 mm long; Sc ending just behind fork of Rs; sc–r before fork of Rs, opposite 2/3 of Rs length, and at four times its length before end of Sc; fork of Mb distinctly before fork of Rs; cubital cross-vein opposite fork of Mb; no additional cross-veins in distal radial and medial cells.

Male genitalia (Figs 6E, 6F, 7D): epiandrial lobe broad, only a little narrowed distally; basistyle very broad, with terminal portion incised, forming a small lobe.

Holotype: DEIM 674/1, well preserved male, only distal portion of costal field in right forewing missing (Bitterfeld amber; Hoffeins coll.).

Other material examined: DEIM 1150/2, female without head, portion of thorax, legs and two wings (Hoffeins coll.); MP 1/797/188/01, almost complete female surrounded by milky cloud and with wings partially damaged (donation of J. Serafin).

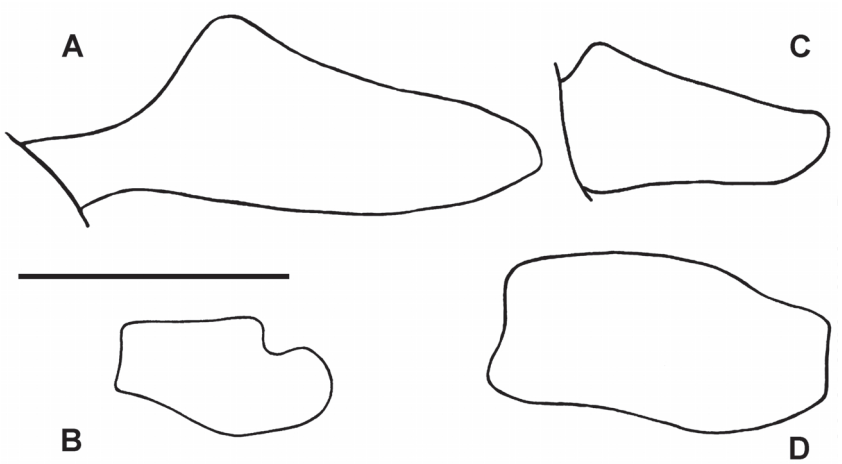

Fig. 7. Epiandrial lobes of Baltic amber Bittacidae in lateral aspect: (A) *Bittacus succinus* Carpenter; (B) *Hylobittacus fossilis* (Carpenter); (C) *Hylobittacus minimus* (Carpenter); (D) *Hylobittacus picteti* sp. n. Scale bar = 1 mm.

Remarks: *H. picteti* sp. n. resembles *H. fossilis* in wing venation, but differs significantly from the latter in epiandrial lobe morphology (Figs 6E, 6F, 7D).

The holotype is from the Saxonian (or Bitterfeld) amber from Saxonia, Germany. Although Saxonian amber has been found in younger sediments, Weitschat and Wichard (2002) state that this is most likely Baltic amber, which was re-deposited several times.

DISCUSSION

Over the last two decades there has been a growing interest in amber inclusions and an increase in scientific literature related to this topic. As a result of this, museum and private collections of amber fossils are steadily growing. However, studies on this rich source of material are hindered by the lack of thorough revisions of genera and families, in the extant fauna of the world. There are several factors which either delay such studies or make them impossible:

1. The number of specialists is insufficient and existing numbers are dwindling.
2. Many holotypes described at the end of the nineteenth and beginning of the twentieth centuries are lost or destroyed.
3. Some material, especially in private collections, is not available. Even if it is known and examined, it should be used with caution, because of the uncertain fate of private collections, which may be sold or lost. The International Code of Zoological Nomenclature (I.C.Z.N. 1999, Recommendation 16C) recommends deposition of type specimens in an institution with facilities for preserving them and making them available for study.

This study has been successful despite these difficulties. As a result of this study, the number of bittacid specimens described has more than doubled. This is encouraging, since this family is generally poorly represented in the fossil state, both in resins and sediments.

It is interesting that in the Baltic amber only a single specimen (and species) was found with two pterostigmal cross veins, while all remaining specimens have only one.

This sample of the bittacid amber fauna, however small, may represent true dominance of this form in the Eocene amber forest. Among Recent representatives the reverse proportion is observed: most species of *Bittacus* have two pterostigmal cross veins, while one cross vein is present only in a few species of this genus, scattered over the world, and in one species of *Hylobittacus*. A revision of both genera is thus necessary, in order to determine the importance of this character for the systematics of Bittacidae.

The small degree of variation in the wing venation of Bittacidae in the Baltic amber is most remarkable. It is however difficult to compare this with Recent species, as there are no studies on the patterns of wing venation. It may only be noted that Carpenter must have considered intraspecific variation great, as he included various patterns in one species (Carpenter 1954).

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Paleopsychoda zherikhini, a new Cretaceous species of moth flies from Taimyr amber (Diptera: Psychodidae: Psychodinae)

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ABSTRACT

Paleopsychoda zherikhini sp. n. is described from the mid-Cretaceous amber of Taimyr (Siberia, Russia). The discovery of this psychodid fly shows a broad distribution of this genus in the Early and Late Cretaceous and improves our knowledge of the biodiversity and the evolution of moth flies.

KEY WORDS: Insecta, Diptera, Psychodidae, new species, Late Cretaceous, Russia, Siberia, Taimyr, Zhdanikha, amber.

INTRODUCTION

The genus *Paleopsychoda* includes three species, *P. solignaci* Azar *et al*., 1999, *P. jacquelinea* Azar *et al*., 1999 and *P. inexpectata* Azar & Nel, 2002, from the Lebanese Lower Cretaceous amber. Phlebotomine-like mouthparts suggest that members of this extinct genus were probably blood feeders.

The studied material comes from the locality of Zhdanikha, which is on the left bank of the Khatanga River, 1 km upstream of its mouth, Taimyr Peninsula, Western Siberia, Russia (Fig. 1). The fossil resin has been collected from the middle part of the Begichev Formation. The *History of Insects* (Eskov 2002: 444) reports that the arthropod inclusions

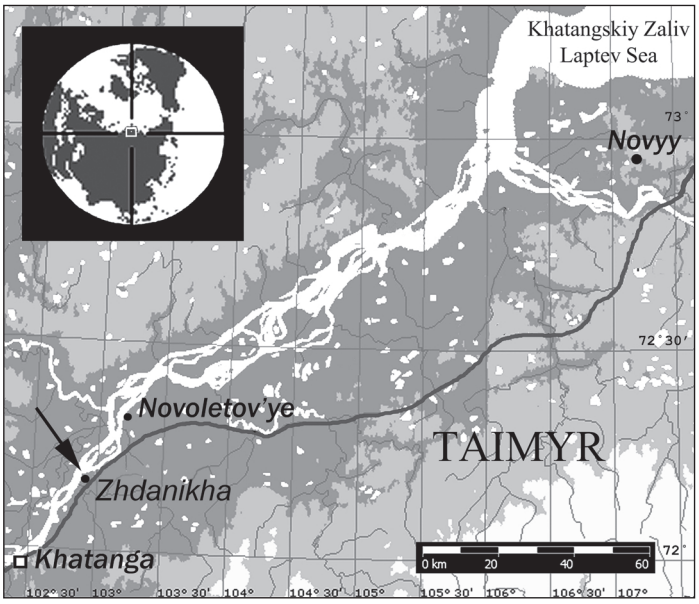


Fig. 1. Map showing the locality of Zhdanikha, where the amber was found.

in this amber have been discovered in four localities in the Khatanga River basin (Eastern Taimyr). The Begichev Formation of the mid-Cretaceous (Albian to Early Cenomanian) age is represented by the fluvial and deltaic sands with lenses of lignitised wood containing the retinite. Although inclusions in this amber are relatively rare, over 40 arthropods have been found, representing seven orders, with the Diptera being dominant (Zherikhin & Sukatsheva 1973; Zherikhin 1978).

Below, we follow the wing venation nomenclature of McAlpine (1986) and the nomenclature of genital appendages proposed by the Computer-aided Identification of Phlebotomine Sandflies of America (CIPA group project, University of Paris-6, Jussieu), available on the web site http://cipa.snv.jussieu.fr. The type material of the newly described species is deposited in the Paleontological Institute, Russian Academy of Sciences, Moscow.

TAXONOMY

Family Psychodidae Bigot, 1854
Subfamily Psychodinae ?
Genus *Paleopsychoda* Azar *et al*., 1999

Type species: *Paleopsychoda solignaci* Azar *et al*., 1999.
Other species: *P. jacquelinea* Azar *et al*., 1999; *P. inexpectata* Azar & Nel, 2002; *P. zherikhini* sp. n.

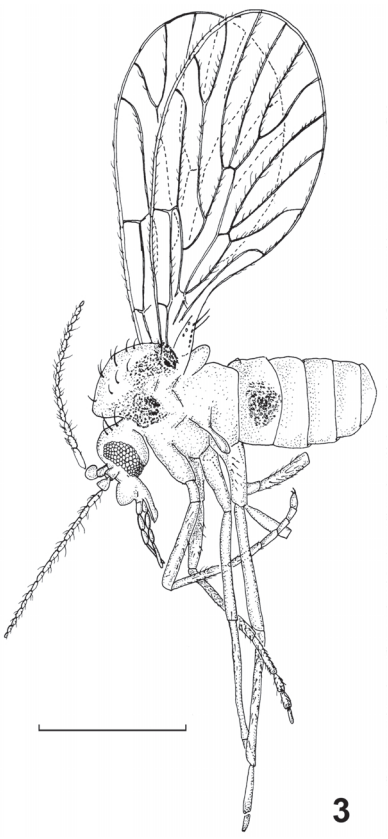
Paleopsychoda zherikhini sp. n.

Figs 2–10

Etymology: In memory of Prof. Vladimir Zherikhin, who was a friend of the senior author and a great authority in palaeoentomology.

Diagnosis: Eyebridge incomplete. Mouthparts well developed and phlebotomine-like. Maxillary palp 4-segmented, with last palpomere twice as long as others. Third and fourth palpomeres with secondary annulations over their entire length. Antenna with 15 flagellomeres, the last one being reduced and drop-like.

Description: Mouthparts well developed, equal in length to head (Figs 4–7), palp 0.45 mm long, with four palpomeres. Eyes forming weak and incomplete eyebridge, separated by distance of 0.125 mm. Antenna 0.675 mm long, with 15 flagellomeres. First flagellomere nearly twice as long as others and terminal flagellomere reduced and drop-like. Scape cylindrical, 0.055 mm long and 0.035 mm wide. Pedicel nearly globular, about 0.045 mm long and wide. All flagellomeres bearing curved setae. Wing 1.2 mm long, 0.55 mm wide, hyaline (Fig. 8). Humeral vein reaching costal margin at 0.125 mm from wing base. Subcostal vein (Sc) distally fused with R1 at almost right angles, 0.465 mm from wing base, and with crossvein reaching costal margin. R1 reaching costal margin 0.885 mm from wing base. Rs separated from R1 at 0.335 mm from wing base, 0.09 mm basad of M1+2 and M3 fork. Rs four-branched, with all its branches extending to wing margin. Rs bifurcating into R2+3 and R4+5 0.45 mm distad of wing base. R2 and R3 separating 0.85 mm distally. R4 and R5 separating 0.175 mm distad of R2+3 base. R4 curved. R5 with strong angle in its basal part and distally very slightly curved. Crossvein r–m 0.635 mm distad of wing base. M1+2 and M3 diverging 0.275

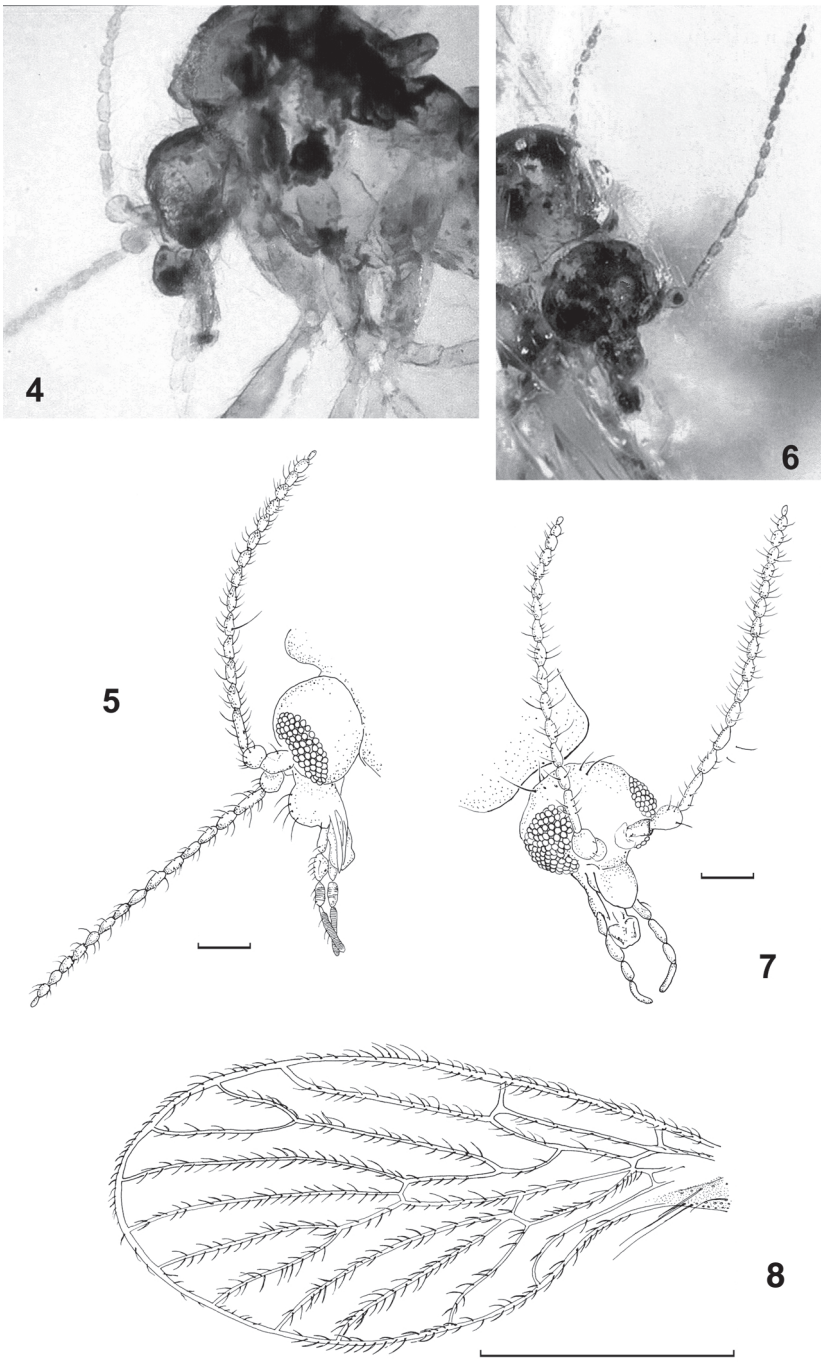


Figs 2, 3. *Paleopsychoda zherikhini* sp. n., holotype no. 3308/13: (2) general appearance, (3) details of body structure. Scale bar 0.5 mm.

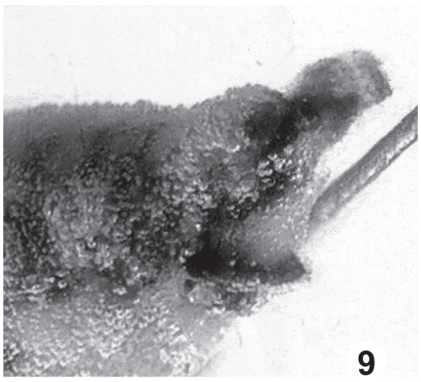
mm distad of arculus. M1 and M2 bifurcating 0.36 mm distad of M1+2 base. M1 distally nearly straight. M2 slightly shorter than M1. M3 reaching wing margin at nearly 0.8 mm from wing base. CuA1 separating from CuA 0.395 mm distad of wing base. CuA2 rather developed, curved distally, 0.24 mm long. A1 well developed and reaching posterior wing margin. All main veins and wing margin bearing long macrotrichiae. Halteres 0.18 mm long. Knob 0.06 mm long and 0.025 mm wide. Stem 0.12 mm long. Thorax 0.5 mm long, 0.45 mm high. Pronotum gibbous with its upper surface bearing few long setae. Legs very long, distinctly longer than entire body. Abdomen 0.48 mm long excluding genital appendages, 0.31 mm wide. Dorsal surfaces of all abdominal segments bearing few setae. Female genital appendages (Figs 9, 10) covered by a thin layer of small gas bubbles but nevertheless discernable. Subgenital plate elongate, 0.085 mm long. Cerci rounded, 0.055 mm long and 0.06 mm wide. Subgenital plate and cerci bearing fine and dense setae.

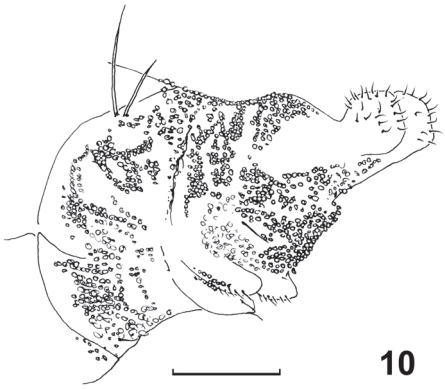
Holotype: specimen no. 3308/13, sex unknown; locality of Zhdanikha; mid-Cretaceous, Begichev Formation.

Paratypes: specimens no. 3308/14, sex unknown, and no. 3308/15, female, from the same locality and horizon as the holotype.



Figs 4–8. *Paleopsychoda zherikhini* sp. n.: (4, 5) holotype no. 3308/13: (4) head and thorax in lateral view, (5) structural details of head, lateral view; (6, 7) paratype no. 3308/14: (6) head, (7) structural details of head, frontal view; (8) wing details of holotype no. 3308/13. Scale bars 0.1 mm in Figs 5, 7 and 0.5 mm in Fig. 8.





Figs 9, 10. Female genitalia of *Paleopsychoda zherikhini* sp. n., paratype no. 3308/15: (9) ventro-lateral view, (10) details in ventro-lateral view. Scale bar 0.5 mm.

DISCUSSION

Paleopsychoda zherikhini shares with all other species of this genus general features like the incomplete eyebridge, mouthparts well developed and phlebotomid-like, and antenna with 15 flagellomeres, the last one being reduced and drop like. These characters allow us to attribute *P. zherikhini* to *Paleopsychoda*.

The new species differs from its congeners in having shorter antennae and in the distance between the R2+3 fork (into R2 and R3) and the M1+2 fork (into M1 and M2). In *P. solignaci*, *P. jacquelinea* and *P. inexpectata* this distance is null whereas in *P. zherikhini* the R2+3 fork is more apical. *P. zherikhini* has a developed CuA2 like *P. solignaci*, this vein being longer in *P. jacquelinea* and shorter in *P. inexpectata*. M3 and CuA1 meet at one point in *P. zherikhini* and *P. solignaci*, whereas they are merged for a small distance in *P. jacquelinea*. In *P. inexpectata*, M3 and CuA1 do not meet at all, but there is a small crossvein between them. R2 is nearly half as long as R3 in *P. zherikhini* and *P. inexpectata*; it is slightly longer than one-third of R3 in *P. solignaci*, and it is nearly equal to R3 in *P. jacquelinea*.

Azar *et al*. (1999: 1111) attributed the genus *Paleopsychoda* to the Psychodinae and they integrated it in a cladistic phylogeny (Azar *et al*. 1999: 1131) mainly based on the phylogenetic analysis of Hennig (1972). Nevertheless, they were uncertain of their systematic attribution: "The only uncertainties concern the genera *Phlebotomites* and *Paleopsychoda*, which appear in unresolved polytomies because we failed to define any autapomorphies for these genera" (Azar *et al*. 1999: 1132). Even if the genus *Paleopsychoda* shares a lot of characters with the Psychodinae, its systematic position within the Psychodoidea remains debatable and it demonstrates that the phylogenetic history of this peculiar group is clearly more complicated than what one could expect.

CONCLUSIONS

Paleopsychoda species were originally found in the Early Cretaceous Lebanese amber, which is of Gondwanaland origin. The discovery of *P. zherikhini* in the Laurasian Albian/Cenomanian Taimyr amber indicates that this genus survived at least 25 to 35 My and

provides interesting information on its wide distribution during the Cretaceous. The finding of a new species belonging to the genus *Paleopsychoda* in the Taimyr amber greatly increases our knowledge about biodiversity of psychodids in general and this genus, in particular.

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We extend our thanks to Prof. R. Wagner (Schlitz, Germany) and Dr M. Mostovski (Pietermaritzburg, South Africa) for all their very precious and important comments. We thank our colleagues at the Paleontological Institute of the Russian Academy of Sciences for providing material for this study and their help. We also thank Prof. I. Koubeissy, President of the Lebanese University, where this study was conducted, for all his encouragement and help.

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New chironomid flies in Early Cretaceous Lebanese amber (Diptera: Chironomidae)

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ABSTRACT

The oldest representatives of the Tanypodinae (Macropelopiini, Pentaneurini and Anatopyniini), *Libanopelopia cretacica* gen. et sp. n., *Cretapelopia salomea* gen. et sp. n., *Wadelius libanicus* gen. et sp. n.; the oldest representative of the Orthocladiinae, *Lebanorthocladius furcatus* gen. et sp. n.; and the oldest representatives of the Prodiamesinae, *Libanodiamesa deploegi* gen. et sp. n. and *Cretadiamesa arieli* gen. et sp. n., are described from the Early Cretaceous Lebanese amber. The male of the podonomine *Libanochlites neocomicus* Brundin, previously known only from a female specimen, is described, supporting its allocation to this subfamily. The positions of the previously described Mesozoic taxa attributed to the Chironomidae are discussed. In particular, *Gurvanomyia rohdendorfi* Hong from the Early Cretaceous of China, and *Manlayamyia dabeigouensis* Zhang from the Late Jurassic of China are considered as Diptera *incertae sedis*. The most recent discoveries demonstrate the great antiquity of the recent chironomid subfamilies and tribes and the high morphological stability within this group since the Early Cretaceous.

KEY WORDS: Diptera, Chironomidae, Orthocladiinae, Podonominae, Prodiamesinae, Tanypodinae, Early Cretaceous, Lebanese amber, aquatic, oldest records.

INTRODUCTION

Chironomid flies are common to the Jurassic and Early Cretaceous aquatic insect assemblages (Evenhuis 1994; Sinitshenkova 2002), even if the systematic positions of some of the described taxa remain debatable. Among others, *Gurvanomyia rohdendorfi* Hong, 1992 from the Early Cretaceous of China is based on an adult of unknown sex (genitalia and antennae either unpreserved or poorly preserved) (Hong *et al.* 1992). The original drawing clearly does not correspond to the original photograph. In addition, its allocation to the Chironomidae is not sufficiently supported and thus we consider it to be a Diptera of uncertain position. It will be necessary to re-examine the holotype to clarify its position. *Manlayamyia dabeigouensis* Zhang, 1991 (in fossil genus *Manlayamyia* Kalugina, 1980), from the Late Jurassic of China, is based on male and female adults, and pupae (Kalugina 1980*a*). The allocation of fossil pupae and adults to the same species of chironomid fly is strongly debatable. In this material, originally illustrated by Zhang (1991), the wing venation and body structures crucial in identifying the specimen as a chironomid, rather than a ceratopogonid, are not visible or poorly preserved. Thus, as in the case with *Gurvanomyia rohdendorfi* Hong, 1992, the allocation of *Manlayamyia dabeigouensis* Zhang, 1991 to the Chironomidae remains uncertain. It is a Diptera of uncertain position. *Sinoryctochlus insolitus* Zhang, 1991 (in fossil genus

Sinoryctochlus Zhang, 1991), from the Late Jurassic of China, is based on male and female adults, which, according to the original illustrations by Zhang (1991), have rather poorly preserved wing venation. Kalugina (1985) attributed three new species to the Middle/Late Jurassic genus *Ulaia*, i.e. *U. magna*, *U. montana*, and *U. reducta*, all based on more or less complete pupae. Their allocation to the same genus is very debatable because the pupae lack the genital structures necessary for accurate identification. Similarly, Kalugina (1985) attributed two new species to the Middle/Late Jurassic genus *Jurochlus* Kalugina, 1985, viz. *J. sibiricus* and *J. rigor*, both based on more or less complete pupae. Thus, their allocation to the same genus is also very debatable. Kalugina (1985) also placed her *U. mixta* in the Middle Jurassic genus *Ulaimailonia* Kalugina, 1985 based on a larval specimen, which is difficult to compare to the fossil pupae attributed to *Ulaia*. Finally, Kalugina (1985) described six species in the Early/Middle Jurassic genus *Podonomius* Kalugina, 1985, viz. *P. tugnuicus*, *P. splendidus*, ?*P. simplex*, ?*P. rotundatus*, ?*P. minimus*, and ?*P. undulatus*. Some descriptions are based on adult specimens while others are based on pupae. These allocations may be inaccurate since it is not possible to effectively compare adult specimens with immature instars.

Nevertheless, some specimens of Late Jurassic or Cretaceous Chironomidae are attributed to recent subfamilies, and in some cases, recent tribes. Among others, the recent subfamily Podonominae is represented by *Libanochlites neocomicus* Brundin, 1976 from the Early Cretaceous Lebanese amber. Some other taxa are also currently attributed to this subfamily, although they are more poorly preserved in lacustrine deposits. Thus, Kalugina (1985) described five new Middle/Late Jurassic species in the fossil genus *Oryctochlus* Kalugina, 1985, viz. *O. affinis*, *O. longilobus*, *O. minor*, *O. minutus* and *O. vulcanus*. Kalugina allocated certain larvae, pupae and adults to a particular species. This deduction is strongly debatable, since it is not possible to compare larval, pupal and adult characters. In addition, the adult specimens are not very well preserved. *Oryctochlus contiguus* Zhang, 1991, from the Late Jurassic of China, is based on both male and female adults, better preserved than those of *M. dabeigouensis*. Thus it is likely that this species is a true chironomid. The recent subfamily Aphroteniinae is represented by *Electrotenia* Kalugina, 1980, with one species *E. brundini* Kalugina, 1980, based on an adult male and female from the Late Cretaceous Taymir amber from North Siberia (Kalugina 1980*b*). The recent subfamily Diamesinae is represented by *Cretodiamesa* Kalugina, 1976, with one species *C. taimyrica* Kalugina, 1976, based on an adult male and female from Late Cretaceous Taimyr amber (Kalugina 1976). The recent subfamily Orthocladiinae is represented by *Metriocnemus cretatus* Boesel, 1937, *Smittia veta* Boesel, 1937 and *Spaniotoma conservata* Boesel, 1937 from the Late Cretaceous Canadian amber (Boesel 1937). However, all of these genera now have a different content and definition, with *Spaniotoma* regarded as a *nomen dubium*.

The Mesozoic Tanypodinae are represented by more uncertain taxa. Kalugina (1985) described *M. pallida* in the Middle Jurassic genus *Mailonia* Kalugina, 1985, based on a pupa. She described *T. stygialis* in the Middle Jurassic genus *Tophocladius* Kalugina, 1985, based on adults, and attributed it to the tanypodine tribe Macropelopiini. This tribal allocation is weakly supported as these fossils do not show the tarsal structures and the position of the cubital fork characteristic of Macropelopiini. Kalugina made no comparisons with the recent tanypodine genera. She also placed her "*T*". *gorchonensis*

in the Middle Jurassic genus "*Tanypodites*" Kalugina, 1985, based on a very incomplete adult male, thus attributing it to the ?Tanypodinae. Kalugina (1986) described the fossil genus *Gurvanomyia* with two species, *G. magna* and *G. moderata*, from the Late Jurassic/Early Cretaceous of Mongolia, based on incomplete adults with poorly preserved wing venation. Kalugina (1986) also described *Shinlustia irae* from the Early Cretaceous of Mongolia on the basis of a poorly preserved adult.

Although the Chironomidae are not rare in the early Cretaceous Lebanese amber (Azar 2000), to date only one genus and species has been described. Herewith we describe the first fossil representatives of the Pentaneurini (Tanypodinae), the oldest representatives of the Orthocladiinae and Prodiamesinae, and the male of the podonomine genus *Libanochlites*, previously known only from a female specimen. The Mesozoic taxa currently attributed to the Tanypodinae cannot be compared with our material since those previously described taxa are all based on poorly preserved fossils.

MATERIAL AND METHODS

The studied specimens originate from the various outcrops of Lebanese amber (Azar 2000). Amber pieces were embedded in epoxy resin. All types and other examined specimens are provisionally deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN).

We follow the body and wing venation terminology of Oliver and Dillon (1989).

TAXONOMY

Family Chironomidae Newman, 1834
Subfamily Tanypodinae Skuse, 1889 (see Spies 2005)
Tribe Pentaneurini Hennig, 1950 or Macropelopiini Zavrel, 1929

Genus **Libanopelopia** gen. n.

Etymology: After Lebanon and the recent genus *Telopelopia*.

Type species: *Libanopelopia cretacica* sp. n., by present designation.

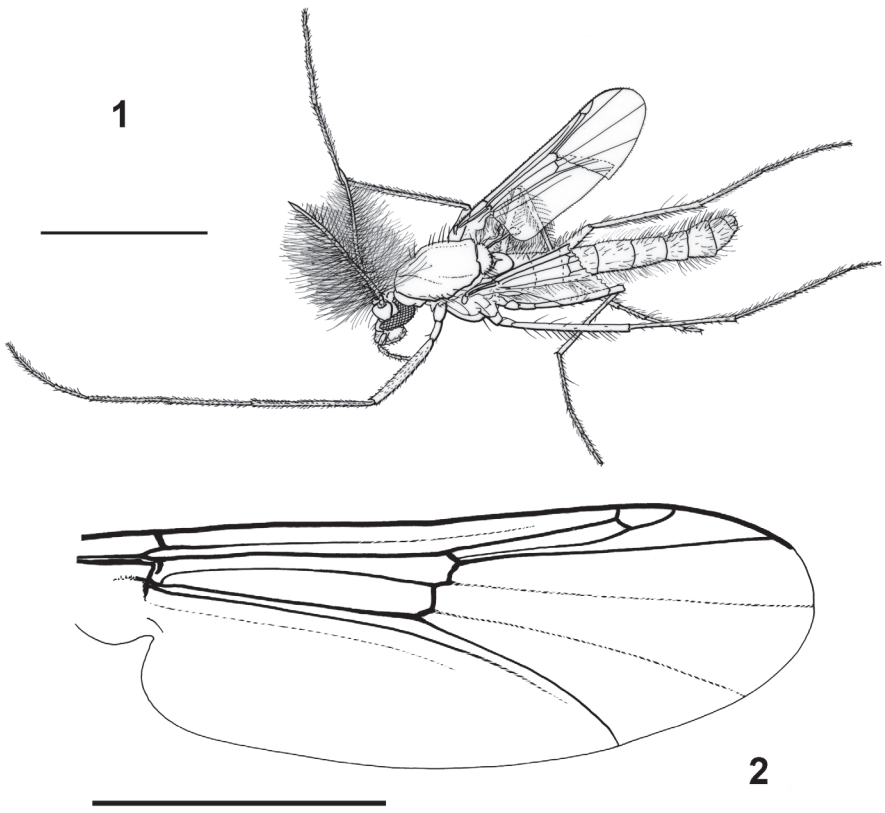
Diagnosis. Eye bare. Costa produced beyond R_{4+5} by a distance less than the length of cross-vein RM, ending slightly before M_{1+2}; R_{2+3} well separated from R_1 and R_{4+5}, apically divided into R_2 and R_3, with R_2 rather long and well distinct. Hind tibial comb disposed in one row; two tibial spurs on both mid and hind leg with lateral comb-like teeth, outer tibial spur half as long as inner spur, those of hind legs not flattened. Inferior volsella small or absent; gonostylus distinctly shorter than gonocoxite.

Libanopelopia cretacica sp. n.

Figs 1–3

Etymology: After the Cretaceous period.

Description: Head deformed, 0.4 mm long. Ocelli absent. Antenna 0.88 mm long, much longer than head, distinctly hairy; scape broad and short, rounded; pedicel very short; 14 flagellomeres, flagellomeres 1–13 covered with long setae (shortest 0.01 mm long, longest 0.48 mm long), flagellomere 13 very long (0.5 mm), flagellomere 14 evenly tapering from base to apical nipple, twice as long as broad at base. Eye bare, deformed



Figs 1–3. *Libanopelopia cretacica* gen. et sp. n., holotype HAR 2: (1) details of general habitus; (2) wing; (3) general habitus. Scale bars = 1 mm in Figs 1, 3 and 0.5 mm in Fig. 2.

but with an apically expanded dorso-medial extension, with 4 rows of ommatidia at minimum width. Clypeus 0.14 mm long, with few dorsal setae. Mouthparts lacking functional mandibles; all palpomeres with numerous setae, but the second with 2 distinctly longer setae. No postocular setae; 5 or 6 long frontal setae; inner vertical and outer vertical setae not visible.

Thorax 0.7 mm long, 0.33 mm wide, 0.5 mm high; postnotum bare, with a very distinct longitudinal median groove; scutellum bare but with 8 long setae on its posterior margin; scutal tubercle absent; 1 supraalar, 3 prealars, a series of 7 or 8 anterior acrostichals, a series of few aligned dorsocentrals; postanepisternal setae absent.

Wing macropterous, 1.44 mm long, 0.48 mm wide, hyaline, covered with macrotrichia. Costa ending just beyond insertion of last branch of radius, produced by 0.06 mm, shorter than cross-vein RM, ending slightly before M_{1+2}. Radius with 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} apically forked into R_2 and R_3; R_2 0.04 mm long, ending in R_1, R_3 0.1 mm long, ending in costa. Only M_{1+2} and M_{3+4} present; cross-vein MCu present; cross-vein RM 0.04 mm distal of MCu; cubital fork 0.02 mm proximal to cross-vein MCu. Anal vein An_2 absent. Halter 0.22 mm long.

Fore femur length 0.72 mm, tibia 0.82 mm, tarsus 1.06 mm; mid femur 0.71 mm, tibia 0.66 mm, tarsus 0.9 mm; hind femur 0.54 mm, tibia 0.70 mm, tarsus 0.96 mm. Tibial spur formula 1–2–2, all with lateral teeth, comb-like; those of hind legs not flattened – a state similar to extant *Derotanypus* (see Murray & Fittkau 1989, fig. 5.13D); 2 hind-leg tibial spurs, 0.04 mm and 0.02 mm long respectively. Fourth tarsomeres of all legs cylindrical, not cordiform. Middle leg claw simple as in front and hind legs; not pectinate. Hind tibial comb disposed in 1 row.

Abdomen 1.6 mm long, 0.24 mm wide. Gonostylus nearly bare, strongly curved, short, 0.07 mm long, 0.03 mm wide, distinctly shorter than gonocoxite; gonocoxite 0.12 mm long, 0.06 mm wide, with numerous long setae. Anal point very smooth, broad and small (0.7 mm wide at base, 0.02 mm deep?). Inferior volsella not visible; if present, very small.

Holotype: ♂ HAR 2. LEBANON: *South Lebanon district* [*Mouhafazit Loubnan el-Janoubi*]: Caza Jezzine, locality between villages Homsiyyeh, Aazour and Roum; Early Cretaceous, Neocomian sandstone (D. Azar coll.).

Note: This amber outcrop was discovered in July 1999 by one of the authors (D.A.), but biological inclusions were only found when the exact layer bearing amber was located in June 2004. The present chironomid fly is the first fossil insect to be described from this outcrop.

Discussion: According to the key to dipteran families (McAlpine 1981), this fossil can be included within Chironomidae because of the combination of the following characters: anal vein An2 absent; radius with only three branches R_1, R_{2+3}, and R_{4+5}, costa ending just beyond insertion of last branch of radius; ocelli absent; antennae much longer than head, and distinctly hairy; wings narrow; only M_{1+2} and M_{3+4} present; mouthparts lacking functional mandibles; postnotum with a very distinct longitudinal groove. According to the Nearctic genera keys of Oliver (1981) and the key to Holarctic subfamilies of Oliver and Dillon (1989) and to Palaearctic subfamilies in Sæther *et al.* (2000), this fossil belongs to the subfamily Tanypodinae because of the combination of the following characters: macropterous, wing extending posterior to first abdominal segment; cross-vein MCu present; R_{2+3} present, apically forked into R_2 and R_3; postnotum with longitudinal groove; wing covered with macrotrichia.

Sæther (2000*a*) proposed a phylogeny of the chironomid subfamilies. He considered the Tanypodinae as a part of the semifamily Tanypodoinae (= Tanypodinae + Usambaromyiinae + Podonominae + Aphroteniinae), mainly characterised by the presence of a gonotergite in male adults formed by the fusion of tergite IX, laterosternite IX and sternite IX. Unfortunately, the laterosternite IX is not visible in our fossil.

Nevertheless, the specimen can be attributed to the clade (Tanypodinae + Usambaromyiinae) because it shows the main synapomorphy, i.e. "tibial spurs with lateral teeth, comb-like" (Sæther 2000*a*). Affinities with the Usambaromyiinae (Andersen & Sæther 1994) can be excluded because of the presence of vein MCu, tarsomere 4 elongate and not cordiform, and claw of middle legs simple, as in front and hind legs and not pectinate.

Ansorge (1999) proposed a fossil Liassic subfamily Aenneinae, also known from the late Triassic (Krzemiński & Jarzembowski 1999), based on the presence of a long basal part of Rs (plesiomorphy), not present in our fossil. Ansorge (1999) considered Aenneinae to be a possible sister group of a clade comprising other chironomid subfamilies; however, he appears to have ignored the Telmatogetoniinae and some other subfamilies.

Kalugina (1993) erected the Cretaceous fossil subfamily Ulaiinae, based on the genus *Ulaia*, with three species, *U. communis* (pupa and an adult wing), ?*U. magna* (pupa), and *U. kangilica* (pupa). As it is impossible to rear a fossil pupa, the allocation of a pupa and an adult wing to the same species is problematic. The wing attributed to *U. communis* is of a tanypodine-type. It differs from our fossil in that its R_2 is longer than R_3. Thus affinities with this genus and subfamily can be excluded. Furthermore, the validity of this fossil subfamily remains debatable.

According to the key to Nearctic tanypodine tribes and genera of Oliver (1981) and to Fittkau (1962), *Libanopelopia* gen. n. falls in the Pentaneurini because of the following characters: fourth tarsomeres cylindrical, not cordiform; cubital fork proximal to cross-vein MCu; costa produced beyond the radius by distance less than length of cross-vein RM; postanepisternal setae absent; postnotal setae absent; tibial spurs of hind legs not flattened. However, there are no recent Pentaneurini which bear the configuration of the R veins found in *Libanopelopia*. Apart from the short costal extension, the overall wing venation conforms to the tribe Macropelopiini, particularly in the shape of radial veins. The costal extension is quite variable and obviously less important than the overall wing venation. We thus consider the possibility of the genus belonging to the tribe Macropelopiini.

In the keys to Tanypodinae by Murray and Fittkau (1989) and Sæther *et al.* (2000), *Libanopelopia* keys to couplet 32 and couplet 44 respectively, since vein MCu is placed beyond FCu, the costa is produced beyond the radius by a distance less than the length of RM and ending slightly before M_{1+2}, the gonostylus is short, volsellae appear to be absent, the gonostylus is not robust and has parallel sides, the claws are not spatulate, and the eyes are bare. Included in couplet 32 are the pentaneurine genera *Zavrelimyia* Fittkau, 1962, *Reomyia* Roback, 1987, *Krenopelopia* Fittkau, 1962 and *Telmatopelopia* Fittkau, 1962 (Roback 1987). However, unlike *Libanopelopia,* all these genera have a reduced R_2, and veins R_1 and R_{2+3} are very closely parallel. In addition, *Zavrelimyia* has an indistinct R_3 which does not reach the costa. *Reomyia* has a scutal tubercle and a gonostylus which is not strongly curved. In *Krenopelopia,* the costa ends above or slightly beyond M_{1+2} and the gonostylus is about three quarters the length of the

gonostylus. *Telmatopelopia* has a gently curved gonostylus but otherwise, among the species included in couplet 32, it appears to be the genus most similar to *Libanopelopia.*

If the short costal extension is disregarded, *Libanopelopia* keys to the macropelopiine genus *Derotanypus* Roback, 1971 (Murray & Fittkau 1989; Sæther *et al.* 2000), since vein MCu is placed beyond FCu, the tibial spurs have lateral teeth, the postnotals are absent and tibial combs are present only on the hind legs. *Libanopelopia* differs from the genus *Derotanypus* Roback, 1971 in the presence of a shorter costal extension and an unequal length of the tibial spurs.

Tribe Pentaneurini Hennig, 1950

Genus **Cretapelopia** gen. n.

Etymology: After Cretaceous and *Pelopia*.

Type species: *Cretapelopia salomea* sp. n., by present designation.

Diagnosis: Postnotum with numerous long setae and a very distinct longitudinal median groove; scutal tubercle absent; scutellum with numerous long setae. Costa ending just beyond the apex of R_{4+5}, not produced well beyond it, almost reaching wing apex opposite to apex of M_{1+2}; R_2 very short, and veins R_1 and R_{2+3} very closely parallel. Apical brush of strong setae on tarsomere 3 of mid leg absent; all tibial spurs very long and of subequal length, with lateral comb-like teeth. Distal half of gonostylus straight and tapering at apex; anal point sharp and long; gonocoxite rounded.

Cretapelopia salomea sp. n.

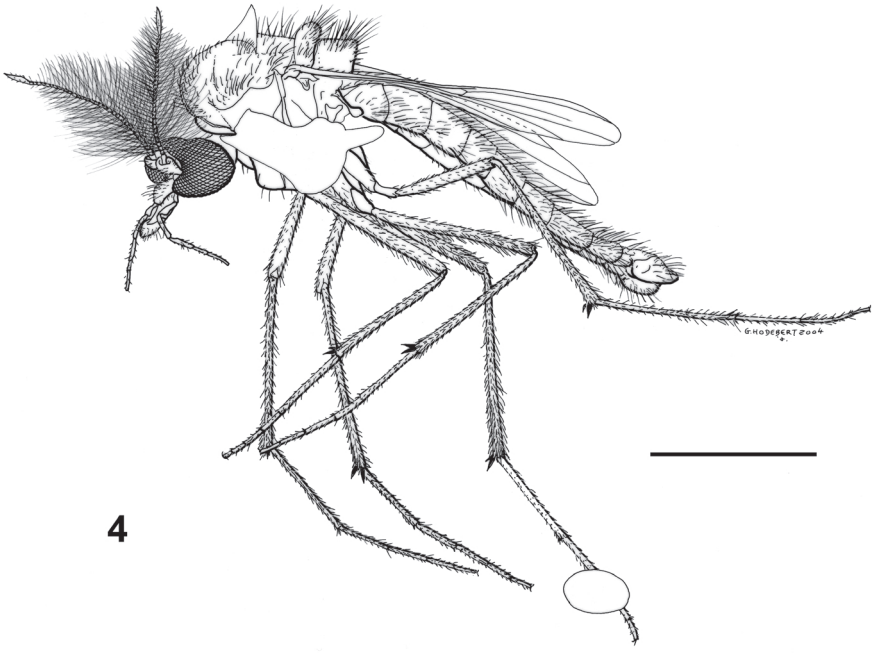
Figs 4–6

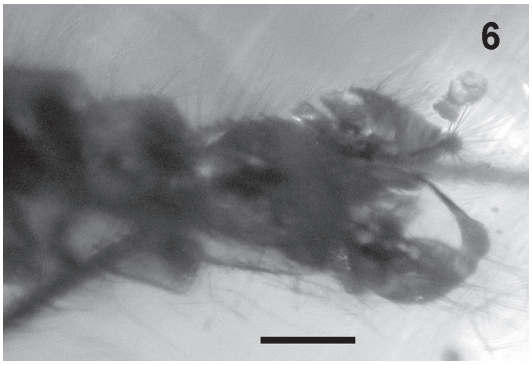
Etymology: After Salomé, daughter of one of the authors (I.V.).

Description: Head 0.82 mm long, 0.55 mm wide. Ocelli absent. Antenna 1.2 mm long, much longer than head, distinctly hairy, 14 flagellomeres; flagellomeres 1–13 covered with long setae (shortest 0.04 mm long, longest 0.5 mm long), scape broad and short, rounded, pedicel very short, flagellomere 13 very long (0.1 mm), flagellomere 14 evenly tapering from base to apical nipple, 0.17 mm long, 9 times as long as broad at base. Eye bare, deformed but with an apically-expanded dorso-medial extension, with 7 rows of ommatidia at minimum width. Clypeus 0.13 long with few dorsal setae. Mouthparts lacking functional mandible, labium 0.39 mm long; palpomeres with numerous setae, all approximately the same length. A row of short postocular setae; frontal, inner vertical and outer vertical setae not visible.

Thorax 1.14 mm long, 0.64 mm wide, 0.84 mm high; postnotum with numerous long setae and very distinct longitudinal median groove; numerous prealar and supraalar setae; series of about 10 anterior acrostichals; series of few poorly aligned dorsocentrals; postanepisternal setae present.

Wing macropterous, 2.32 mm long, 0.65 mm wide, hyaline, and covered with macrotrichia. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} apically forked into R_2 and R_3; R_2 0.06 mm long, ending in R_1, R_3 0.16 mm long, ending in costa. Costa produced beyond insertion of last radial branch by 0.04 mm, distinctly shorter than cross-vein RM. Only M_{1+2} and M_{3+4} present; cross-vein





Figs 4–6. *Cretapelopia salomea* gen. et sp. n., holotype 309: (4) details of general habitus, scale bar = 1 mm; (5) wing, scale bar = 0.5 mm; (6) male genitalia, scale bar = 0.2 mm.

MCu present; cubital fork proximal to cross-vein MCu; cross-vein RM 0.03 mm slightly distal of MCu. Anal vein An_2 absent. Halter 0.36 mm long.

Fore femur length 0.82 mm, tibia 1.1 mm, tarsus 1.8 mm; mid femur 1.14 mm, tibia 1.08 mm, tarsus 1.34 mm; hind femur 1.04 mm, tibia 1.08 mm, tarsus 1.26 mm. Tibial spur formula 1–2–2; all spurs 0.08 mm long, with lateral comb-like teeth, (similar to those of extant genus *Derotanypus*). Fourth tarsomeres of all legs cylindrical, not cordiform; claw of middle legs simple as in fore and hind legs, not pectinate; no apical brush on tarsomere 3 of middle leg.

Abdomen 2.26 mm long, 0.8 mm wide. Gonostylus strongly curved at base (base width 0.06 mm), with numerous long, strong setae, and distally very long (0.16 mm), straight, nearly as long as gonocoxite and tapering at apex; gonocoxite rounded, (0.2 mm long, 0.15 mm wide), with numerous long setae. Anal point sharp and long, 0.1 mm wide at base, 0.02 mm high. Inferior volsella apparently rounded, covered with setae.

Holotype: Specimen 309, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Paratype: Specimen 295, male, same data as holotype.

Discussion: *Cretapelopia* gen. n. appears to fall into the tribe Pentaneurini (Tanypodinae) for the same reasons as *Libanopelopia* (see above). However, it differs from the latter genus in having very reduced R_2, with veins R_1 and R_{2+3} very closely parallel, thus being in accordance with the wing venation of the Pentaneurini.

In the Tanypodinae keys (Murray & Fittkau 1989; Sæther *et al.* 2000) this new genus keys to couplets 6 and 24 respectively. It will not key further since the costal extension is short while postnotals are present. Disregarding the postnotals, the genus keys to couplets 24 and to *Pentaneura* Philippi, 1865 respectively because of the following characters: vein MCu placed beyond FCu, costa not produced; inferior volsella apparently present and rounded in shape; gonostylus broad and strongly curved at base, but distally long, straight and tapering apically; anal point broader than long; scutal tubercle absent; tibia of middle leg bearing two spurs of equal length; tibial spur formula 1–2–2. The tibial spurs of *Cretapelopia* are very different from those of *Pentaneura* (see Murray & Fittkau 1989). In couplet 24, genera without a scutal tubercle, *Rheopelopia* Fittkau, 1962, *Thienemannimyia* Fittkau, 1962, *Meropelopia* Roback, 1971, and *Arctopelopia* Fittkau, 1962, lack postnotals or anepisternals. In these genera, the costa ends approximately opposite to the apex of M_{1+2}, but R_3 ends almost halfway between R_1 and R_{4+5}. Among the Tanypodinae, only some Anatopyniini and Macropelopiini have postnotals or anepisternals; present in *Cretapelopia*. However, judging from the distribution of the thoracic chaetotaxy in the Orthocladiinae, both basal and advanced genera may have these setae and, at least among the orthoclads, this character appears to be of low phylogenetic value.

Tribe Anatopyniini Fittkau, 1962

Genus **Wadelius** gen. n.

Etymology: After Jean-Marc Wadel, friend of one of the authors (I.V.).

Type species: *Wadelius libanicus* sp. n., by present designation.

Diagnosis: Fourth tarsomere cyclindrical, as long as fifth tarsomere; robust and curved claw-like tibial spurs with no lateral teeth; row of long and rigid setae on inner side of

all femora. R_{2+3} apically divided into R_2 and R_3, with R_2 rather long and well distinct; costa produced slightly distal to apex of R_{4+5}; cubital fork slightly proximal to cross-vein MCu. Postanepisternal and postnotal setae present; scutal tubercle present; pulvilli absent; vertical and postorbital setae uniserial. Gonostylus nearly bare, bifurcated in two equally long and slightly curved appendages, the inner appendage ending in a gonostylar tooth; inferior volsella not visible, if present, very small.

Wadelius libanicus sp. n.

Figs 7, 8

Etymology: After Lebanon.

Description: Head 0.25 mm long, 0.52 high. Ocelli absent. Antenna 0.8 mm long, more than 3 times longer than head, distinctly hairy, with 14 flagellomeres, flagellomeres 1–13 covered with long setae (shortest 0.05 mm long, longest 0.4 mm long), scape broad and short, rounded, pedicel very short, flagellomere 13 long (0.3 mm), flagellomere 14 evenly tapering from base to apical nipple, 0.09 mm long. Eye bare, with apically expanded dorso-medial extension. Clypeus 0.13 mm long, with few dorsal setae. Mouthparts lacking functional mandible; all palpomeres with numerous setae; labium 0.23 mm. Uniserial postocular setae; numerous long frontal setae visible; inner vertical and outer vertical setae not visible.

Thorax 0.93 mm long, 0.92 mm high; antepronotum bare; postnotum bearing long setae and with longitudinal groove; scutal tubercle present; scutellum with broken setae; numerous acrostichals, supraalar and prealar setae; postanepisternal setae present.

Wing macropterous, 1.6 mm long, 0.42 mm wide, hyaline, covered with macrotrichia. Costa ending just beyond insertion of last branch of radius, produced by 0.06 mm, shorter than cross-vein RM. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} clearly visible at base and apex but evanescent in its main part; R_2 0.02 mm long, ending in R_1, R_3 0.15 mm long, ending in costa. Only M_{1+2} and M_{3+4} present; cross-vein MCu present. Cubital fork 0.05 mm proximal to cross-vein MCu; cross-vein RM 0.02 mm distal of MCu. Anal vein An_2 absent. Halter 0.2 mm long.

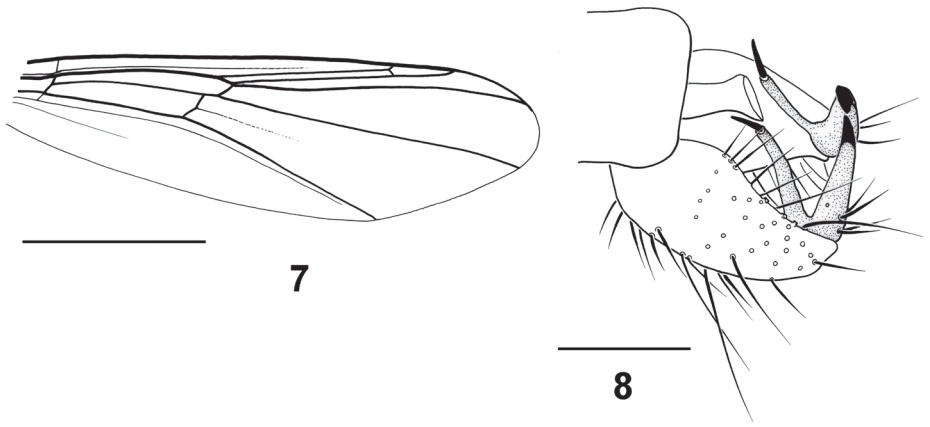
Fore femur length 0.7 mm, tibia 0.82 mm, tarsus 1.08 mm; mid femur 0.7 mm, tibia 0.84 mm, tarsus 0.96 mm; hind femur 0.6 mm, tibia 0.86 mm, tarsus 1.22 mm. Tibial spur formula 1–2–2, with no lateral teeth; two robust and curved claw-like spines on tibial end, 0.04 mm long; hind tibial comb disposed in one row. Fourth tarsomeres of all legs cylindrical, not cordiform; claw simple, not pectinate.

Abdomen 1.4 mm long, 0.4 mm wide. Gonostylus 0.15 mm long; gonocoxite 0.22 mm long, 0.15 mm wide at base, with numerous long setae. Anal point very smooth and broad, though small; 0.04 mm wide at base, 0.05 mm high.

Holotype: Specimen 748A, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Paratype: Specimen 259 (male), same data as holotype.

Discussion: This peculiar tanypodine may deserve a separate tribe. However, one of the most distinct and unique synapomorphies within the Tanypodinae is the comb-like formation of the tibial spurs. The only recent tanypodine without such tibial spurs belongs



Figs 7, 8. *Wadelius libanicus* gen. et sp. n.: (7) wing, holotype 748A, scale bar = 0.5 mm; (8) male genitalia, paratype 259, scale bar = 0.1 mm.

to the tribe Anatopyniini with the single included genus *Anatopynia* Johannsen, 1905. Similarities between *Wadelius* and this tribe also are found in the extensive thoracic chaetotaxy and in the probable absence of an inferior volsella. The wing venation is also similar although the costa is more produced and the cubital fork is more proximal to cross-vein MCu in *Anatopynia*. In addition, unlike *Anatopynia, Wadelius* has a scutal tubercle.

The two genera *Tanypus* Meigen, 1803 and *Nilotanypus* Kieffer, 1923 have very rudimentary comb-like structures, which are very difficult to see. *Wadelius* has similar tibial spurs, but it differs from the former genus in the MCu and cubital fork position, and from the latter in the presence of a divided R_{2+3}. We tentatively attribute *Wadelius* to the Anatopyniini.

Subfamily Orthocladiinae Kieffer, 1911 (see Spies 2005)

Genus **Lebanorthocladius** gen. n.

Etymology: After Lebanon and recent genus *Orthocladius*.

Type species: *Lebanorthocladius furcatus* sp. n., by present designation.

Diagnosis: The genus differs from all other Orthocladiinae in having the following set of characters: wing bare with anal lobe not produced, bare squama, scutal tubercle present, low venarum ratio, very short costal extension, R_{4+5} ending opposite to apex of M_{3+4}, straight Cu_1, large triangular anal point, furcate gonostylus, and hind tibia with one spur only.

Lebanorthocladius furcatus sp. n.

Figs 9–12

Etymology: After the forked gonostylus, characteristic of the male.

Description: Head 0.12 mm long. Ocelli absent. Antenna 0.56 mm long, almost 5 times length of head, distinctly hairy, with 13 flagellomeres covered with long setae (shortest 0.04 mm, longest 0.2 mm), scape broad and short, rounded, pedicel very short,

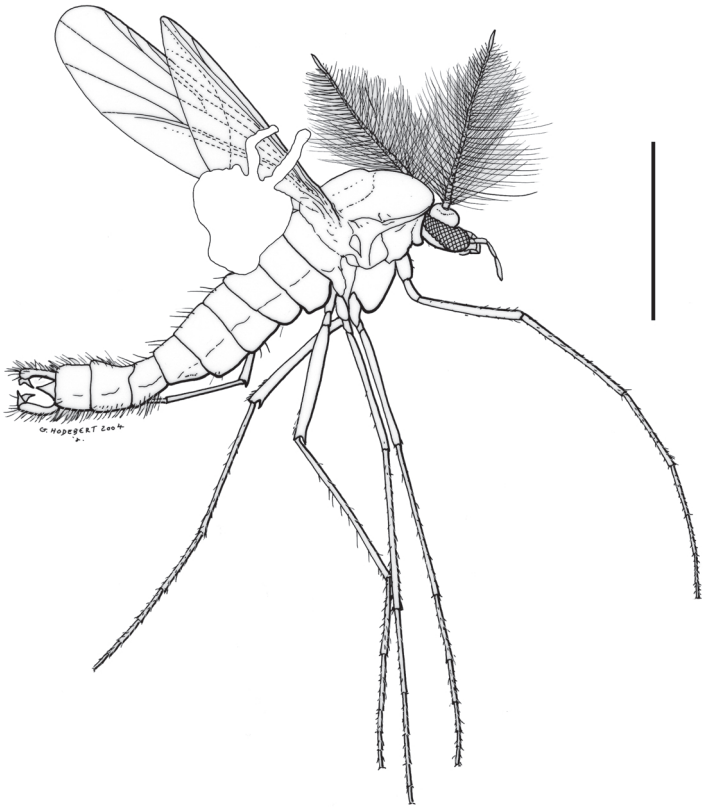
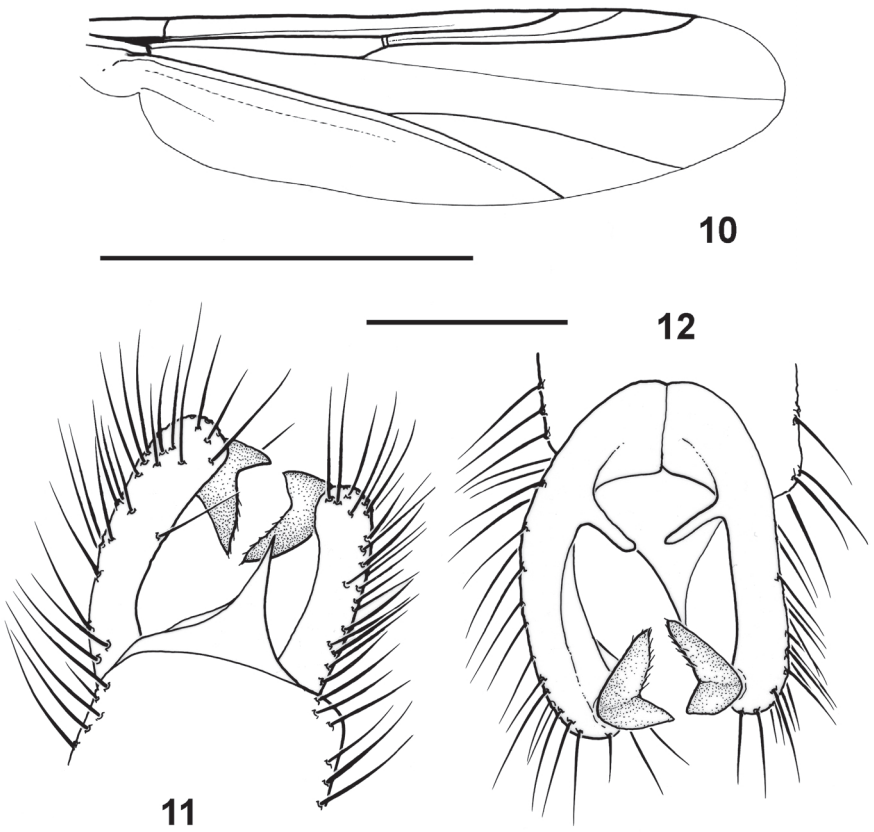


Fig. 9. *Lebanorthocladius furcatus* gen. et sp. n., holotype 5B, general habitus, scale bar = 0.5 mm.

flagellomere 13 very long (0.07 mm). Eye bare, with a small dorso-medial extension, with 3 rows of ommatidia at minimum width. Clypeus with few dorsal setae. Mouthparts lacking functional mandible; 4 palpomeres with numerous setae, all of approximately the same length. Postocular, frontal, inner vertical and outer vertical setae not visible, possibly absent.

Thorax 0.46 mm long, 0.38 mm high; postnotum without visible setae, and no visible longitudinal median groove; surface of scutellum without visible setae; acrostichals and dorsocentrals not visible, probably absent; scutal tubercle present; scutum without median longitudinal groove; epimeron II, posterior mesanepisternum II and dorsal antepronotum bare; no lanceolate setae on scutum; antepronotal lobes not widely separated; anapleural suture distinct.

Wing macropterous, 0.84 mm long, 0.26 mm wide, hyaline, membrane bare. Costa ending just beyond insertion of last branch of radius, distinctly shorter than cross-vein RM. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_{2+3} well separated from R_1 and R_{4+5}, R_{2+3} not forked into R_2 and R_3, ending in costa; R_1 and R_{4+5} elongate, separated from costa until apex; area between costa and R_{4+5} broad. Only M_{1+2} and M_{3+4} present; cross-vein MCu absent; Cu_1 nearly straight. Anal vein An_2 absent; squama without setae. Halter 0.12 mm long.



Figs 10–12. *Lebanorthocladius furcatus* gen. et sp. n., holotype 5B: (10) wing, scale bar = 0.5 mm; (11, 12) dorsal and ventral aspects of male genitalia, scale bar = 0.1 mm.

Fore femur length 0.34 mm, tibia 0.36 mm, tarsus 0.62 mm; mid femur 0.34 mm, tibia 0.44 mm, tarsus 0.5 mm; hind femur 0.38 mm, tibia 0.48 mm, tarsus 0.6 mm. All tarsomeres of fore, middle and hind legs cylindrical, not cordiform; first tarsomere of fore leg distinctly shorter than fore tibia. Hind tibia with one spur and a comb comprised of basally separated spines. Fore coxa not enlarged.

Abdomen 1 mm long, 0.16 mm wide. Gonostylus hinged to gonocoxite and folded inward; short and bifurcate. Gonocoxite with numerous long setae, elongate. Superior (?) volsella large, digitiform; no median volsella and no apparent inferior volsella. Anal point sharp and long, 0.4 mm wide at base, 0.07 mm high.

Holotype: Specimen 5 B, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Other material studied: Specimen 574 I, male, with genital organs missing, from the same locality and possibly also belonging to this species.

Discussion: This species belongs to the subfamily Orthocladiinae because of the following characters: wing present; cross-vein MCu absent; first tarsomere of fore leg distinctly shorter than fore tibia; hind tibia with one spur and a comb comprised of basally separated spines; gonostylus hinged to gonocoxite and folded inward;

antepronotal lobes not widely separated; fore coxa not enlarged; anapleural suture distinct (Oliver 1981; Oliver & Dillon 1989). Except for the key to Holarctic genera of Cranston *et al.* (1989), and the key to Palaearctic genera in Sæther *et al.* (2000), there is no recent world revision of the orthocladiine genera.

Few recent genera have a double, forked, or broad triangular gonostylus, as in *Lebanorthocladius* gen. n., viz. *Aagaardia* Sæther, 2000, *Brillia* Kieffer, 1913, *Diplosmittia* Sæther, 1981, *Plhudsonia* Sæther, 1982, *Propsilocerus* Kieffer, 1923 (= *Tokunagayusurika* Sasa, 1978), *Zalutschia* Lipina, 1939, some *Chaetocladius* Kieffer, 1911, some *Parachaetocladius* Wülker, 1959, and one *Orthocladius* van der Wulp, 1847. *Brillia*, *Diplosmittia*, *Plhudsonia* and *Propsilocerus* have a double gonostylus. *Lebanorthocladius* differs from all of the other genera by the following combination of characters: straight Cu_1, very short costal extension, and R_{4+5} ending opposite to apex of M_{3+4}. All genera except *Aagaardia* also have setae on squama and all lack a scutal tubercle. The volsellae are of the type found in the *Brillia* group of genera, present, for instance, in *Eurycnemus* van der Wulp, 1874 (Fittkau 1974; Sæther 1982, 2000*b*; Chaudhuri & Bhattacharyay 1989; Cranston *et al.* 1989; Kawai 1991; Kobayashi & Sasa 1991; Niitsuma 1991; Sæther & Wang 1992, 1996; Andersen & Sæther 1993*a*, *b*; Sæther & Andersen 1993, 1995; Sæther & Ferrington 1993; Kobayashi 1994; Boothroyd 1994, 1999; Boothroyd & Cranston 1994; Epler & de la Rosa 1995; Ferrington & Sæther 1995; Oliveira *et al.* 1995; Sæther & Kristoffersen 1996; Harrison 1997, 2000; Wiedenbrug & Fittkau 1997; Wang & Sæther 1998, 2002; Cranston & Edward 1999; Sæther & Ekrem 1999; Yamamoto 1999; Cranston 2000; Maheshwari & Maheshwari 2001; Mendes *et al.* 2004*a*, *b*).

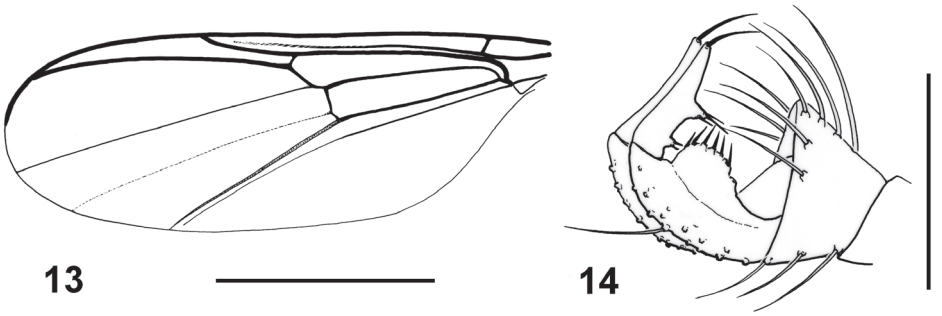
Subfamily Podonominae Thienemann & Edwards, 1937
Genus *Libanochlites* Brundin, 1976
Libanochlites neocomicus Brundin, 1976

Figs 13, 14

Description: Head 0.22 mm long. Ocelli absent. Antenna 0.5 mm long, more than twice as long as head, distinctly hairy, with 14 flagellomeres. Flagellomeres 1–13 covered with long setae (shortest 0.01 mm, longest 0.32 mm), scape broad and short, rounded, pedicel very short. Flagellomere 13 very long (0.07 mm); last 2 flagellomeres slightly more than half as long as remainder of flagellum. Flagellomere 14 long, tapering evenly/consistently from base to apical nipple, less than half as long as flagellomere 13. Eye bare, with a distinct dorso-medial extension. Mouthparts lacking functional mandible; palps very short, with 4 visible palpomeres bearing numerous setae, all of similar length. Postocular, frontal, inner vertical and outer vertical setae not visible; possibly absent.

Thorax 0.48 mm long, 0.25 mm wide, 0.27 mm high; postnotum with few setae, and no visible longitudinal median groove; scutellum with few posterior setae; scutum without median longitudinal groove; dorsal antepronotum with several setae.

Wing macropterous, 0.70 to 0.82 mm long, 0.22 mm wide, hyaline; membrane with setae. Radius with only 2 branches R_1 and R_{4+5}; R_1 short, 0.4 times as long as R_{4+5}. Costa with very long free end, distal of apex of R_{4+5}; cell between R_{4+5} and costa narrow. Cross-vein MCu present, just proximal of RM; fork of Cu just proximal of MCu; Cu_1 not curved apically. Anal vein An_2 absent. Halter 0.1 mm long.



Figs 13, 14. *Libanochlites neocomicus* Brundin, 1976, male, specimen 723: (13) wing, scale bar = 0.3 mm; (14) genitalia, scale bar = 0.1 mm.

Fore femur length 0.44 mm, tibia 0.47 mm, tarsus 0.57 mm; mid femur 0.44 mm, tibia 0.5 mm, tarsus 0.73 mm; hind femur 0.44 mm, tibia 0.49 mm, tarsus 0.76 mm. All tarsomeres of fore, middle and hind legs cylindrical, not cordiform; first tarsomere of fore leg very long, but shorter than fore tibia. Mid and hind tibias with 2 spurs; claw of middle legs simple as in front and hind legs, not pectinate.

Abdomen 1 mm long, 0.07 mm wide. All tergites with 2 long dorsal setae; laterosternite IX fused with tergite IX. Gonostylus swollen at base and extended into a long, slender lobe with a sharp apical spine. Gonocoxite broad, with numerous long setae, elongate.

Material examined: LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Specimens 236, 80, 179, 221, 250 A, 382, 940, 1148, 748 B (9♂), 511, 537, 538, 781 A and B, 1111, 1272B (7♀) and 723 G, H, I , J (1♀, 3♂) from Hammana/Mdeyrij, Caza Baabda (D. Azar coll.). *South Lebanon district* [*Mouhafazit Loubnan el-Janoubi*]: JG 375/3 BM 497, JG 375/5 BM 467 (2♀), JG 375/1 BM 496 (♂) from Jouar Es-Souss (Jezzine outcrop) (Acra coll.). *North Lebanon district*: DAB 6 B (♂) from El-Dabsheh (D. Azar coll.).

Discussion: The male and female specimens examined have the same wing venation as the unique female holotype of *L. neocomicus*, from the outcrop of Jouar Es-Souss near Jezzine, usually known as Jezzine outcrop. The only differences are due to sexual dimorphism (number and structures of the antennomeres, size of the eyes, length of wings). Also the new male specimen (JG 375/1 BM 496) from Jezzine has the same genitalia as those from Hammana. Therefore, we consider that they belong to the same genus and species. The allocation of *Libanochlites* to the subfamily Podonominae was initially based on rather unimportant characters (Brundin 1976). However, the recent discovery of the male has allowed for a more detailed examination of the primary characters, which further supports the position of *Libanochlites* within the Podonominae.

Following the key to Holarctic subfamilies of Oliver and Dillon (1989), *Libanochlites* could fall within the Podonominae or the Buchonomyiinae. However, the laterosternite IX fused with tergite IX in *Libanochlites* is an apomorphy of the group Tanypodoinae and thus excludes affinities with the Buchomomyiinae (Brundin & Sæther 1978; Sæther 2000*a*). Despite having a wing venation very similar to that of *Libanochlites*, the Chilenomyiinae have distinctly different male genital structures (laterosternites IX, gonostyli) (Brundin 1983).

Within the Tanypodoinae, affinities with the Usambaromyiinae can be excluded because of the following characters: presence of vein MCu; tarsomere 4 elongate, not cordiform; claw of middle legs simple as in front and hind legs, not pectinate (Andersen & Sæther 1994). Affinities with the Tanypodinae can be excluded because of the absence

of vein R_{2+3}. Brundin (1976) indicated that this character is an apomorphy of the Podonominae, while the other character—an obsolete anal lobe—is also shared by *Libanochlites*. The Aphroteniinae, the last tanypodoine subfamily, can be excluded because within *Libanochlites,* vein MCu is retained; a character apomorphically absent in the Aphroteniinae. *Libanochlites* also has a narrow cell between R_{4+5} and the costa, an apomorphy absent in the recent Aphroteniinae, but present in Podonominae (Brundin 1966, 1976). The simple gonostylus of *Libanochlites* excludes affinities with the Podonomini and justifies allocation to the Boreochlini, after the female characters, already indicated by Brundin (1976). The most similar recent genus is *Paraboreochlus* Thienemann, 1939, since cross-vein MCu is proximal to cross-vein RM, the pulvilli are not visible and thus probably absent, the tibial spurs are slender, and the eyes are bare (Brundin 1966, 1976; Cranston *et al.* 2002). The broad gonocoxites and narrow elongate gonostyli of *Libanochlites* are also similar to those of this recent genus and yet very different from those of the other recent genera (Brundin 1989). Brundin (1976) separated *Paraboreochlus* from *Libanochlites* based on small differences in the wing venation. In *Paraboreochlus*, R_1 is comparatively longer, the wing itself is slightly longer, and the relative position of MCu with fork of Cu differs from *Libanochlites*. In addition, the male gonostylus of *Paraboreochlus* has small apical megaseta while in *Libanochlites*, the gonostylus has a sharp apical spine.

Subfamily Prodiamesinae Sæther, 1976

Genus **Libanodiamesa** gen. n.

Etymology: After Lebanon and *Diamesa*.

Type species: *Libanodiamesa deploegi* sp. n., by present designation.

Diagnosis: R_{2+3} present, simple. MCu present, in a very basal position, midway between base of M and RM; FCu distal to MCu. Wing membrane without setae. Eye bare.

Libanodiamesa deploegi sp. n.

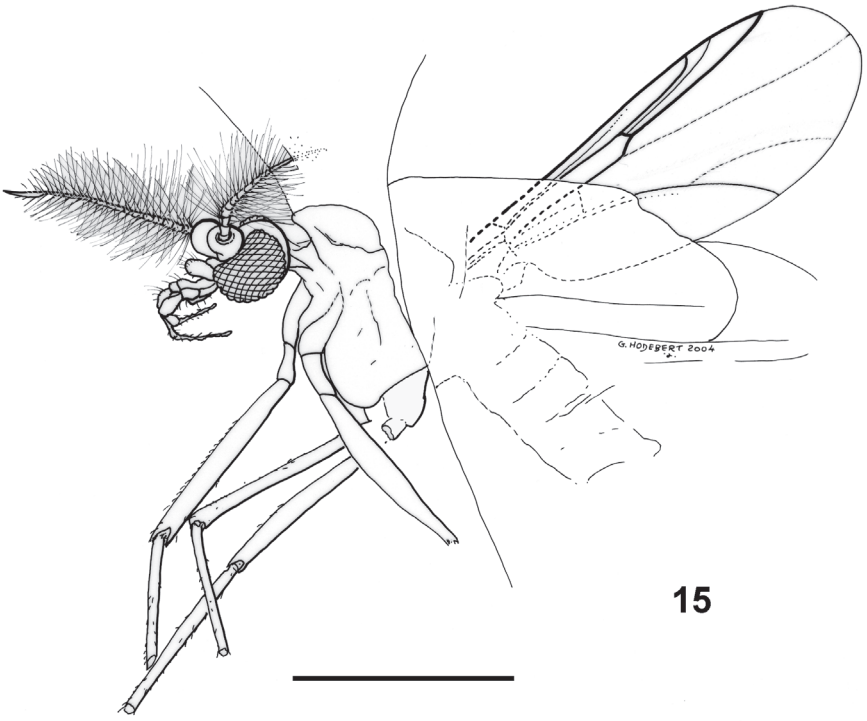
Figs 15–17

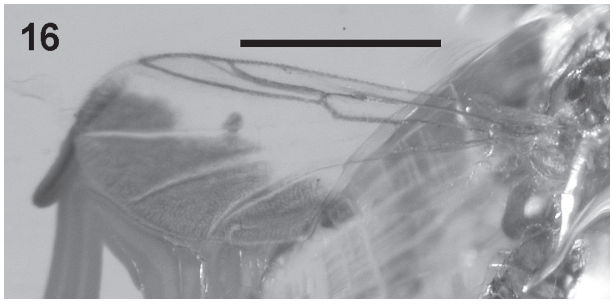
Etymology: After Mr Gaël De Ploeg who with great talent, helped in preparing the material for study.

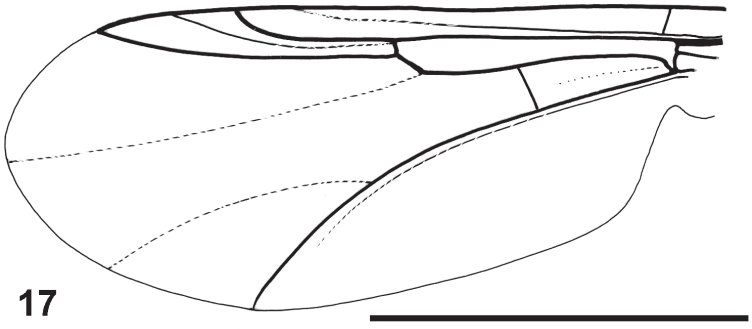
Description: Head 0.26 mm long. Ocelli absent. Antenna 0.5 mm long, almost twice as long as head, distinctly hairy, with 13 flagellomeres, all covered with long setae (shortest 0.04 mm, longest 0.18 mm). Scape broad and short, rounded; pedicel very short. Eye bare, with distinct dorso-medial extension. Mouthparts lacking functional mandible; palps long, with four visible palpomeres bearing numerous setae, last palpomere the narrowest and longest. Two postocular setae; frontal, inner vertical and outer vertical setae not visible, possibly absent.

Thorax 0.8 mm long, 0.6 mm wide, 0.8 mm high. Postnotum, scutellum, scutum without visible setae.

Wing macropterous, 1.2 mm long, 0.41 mm wide, hyaline; membrane without setae. Costa ending at apex of R_{4+5}; radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_1 rather long, 1.66 times as long as R_{4+5}; R_{2+3} simple, closely aligned and parallel to R_1. Cross-vein MCu present, in a very basal position, about midway between base of M and RM.







Figs 15–17. *Libanodiamesa deploegi* gen. et sp. n., holotype 66: (15) general habitus; (16) forewing; (17) details of forewing venation. Scale bars = 0.5 mm.

Fork of Cu nearly opposite RM; Cu_1 curved. Anal vein An_2 absent. Halter 0.14 mm long.

Fore femur length 0.46 mm, mid femur 0.5 mm, hind femur 0.44 mm.

Abdomen narrow, 0.2 mm wide.

Holotype: specimen 66, all tibiae apically broken, tibial spurs destroyed, tarsi missing, apex of abdomen destroyed. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana / Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Discussion. Following the key to Holarctic subfamilies of Oliver and Dillon (1989) and to Palaearctic subfamilies in Sæther *et al.* (2000), *Libanodiamesa* gen. n. falls in the Prodiamesinae because of the combination of the following characters: wing macropterous; MCu present; R_{2+3} present, simple; wing membrane without setae; FCu distal to MCu. Furthermore, *Libanodiamesa* has bare eyes, unlike most recent Diamesinae Kieffer, 1923.

Among the non-Holarctic subfamilies, affinities with the Aphroteniinae are excluded because *Libanodiamesa* has retained MCu and R_{2+3}, but it has a narrow space between R_{4+5} and the costa. In the Usambaromyiinae, MCu is absent. The Chilenomyiinae have a MCu in a basal position (less basal than in *Libanodiamesa*), but no R_{2+3}. Furthermore, unlike *Libanodiamesa*, their wings are uniformly covered with dense hair.

Within the Prodiamesinae, *Libanodiamesa* differs from all recent genera in the much more basal position of MCu, located midway between base of M and RM, and in the $R_{4+5,}$ which ends well basad of the wing apex (Sæther 1989). The lack of genital organs in the holotype of *Libanodiamesa* renders it impossible to predict the relationship of this genus with the other recent genera. *Libanodiamesa* and *Cretadiamesa* gen. n. (see below) are the oldest representatives of the subfamily Prodiamesinae.

Genus **Cretadiamesa** gen. n.

Etymology: After Cretaceous and *Diamesa*.

Type species: *Cretadiamesa arieli* sp. n., by present designation.

Diagnosis: Closely similar to *Libanodiamesa*; the differences with this genus being as follows: veins R_1 and R_{4+5} strongly approximate; R_{2+3} very weakly indicated; apex of R_{4+5} near wing apex; costa ending near wing apex.

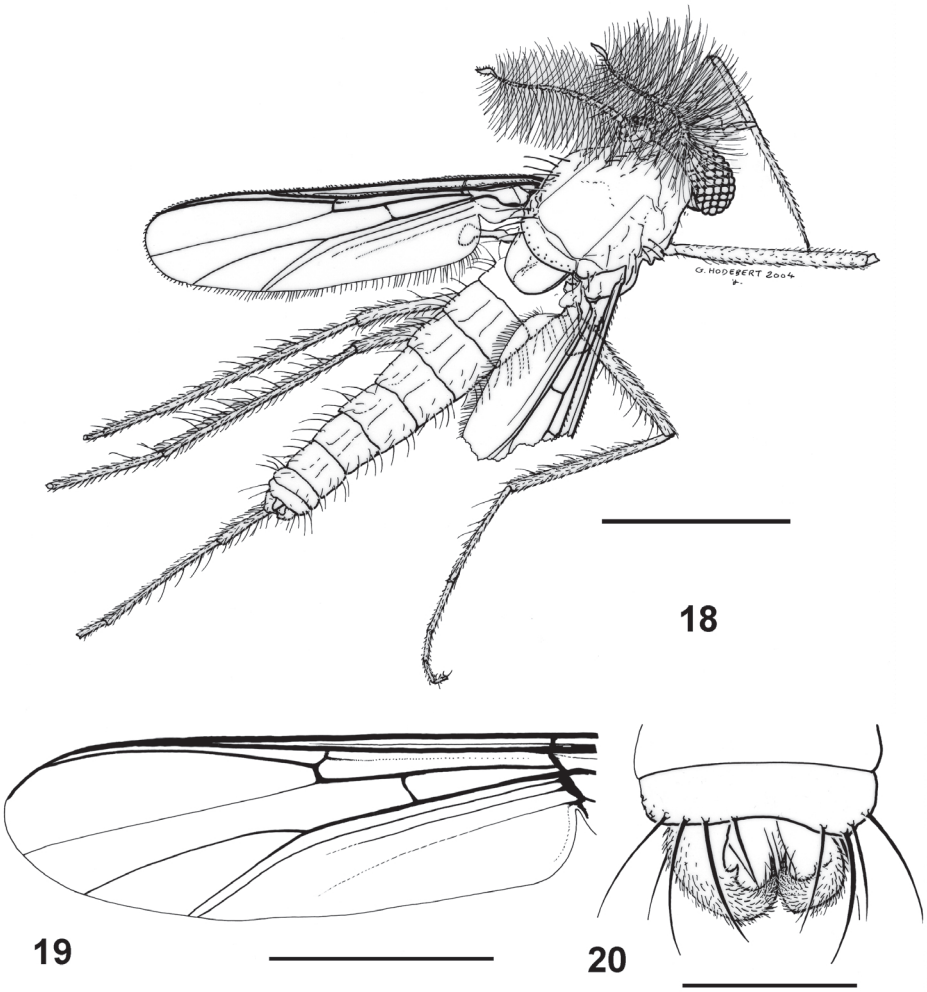
Cretadiamesa arieli sp. n.

Figs 18–20

Etymology: After Ariel, son of one of the authors (I.V.).

Description: Head 0.2 mm long. Ocelli absent. Antenna 0.6 mm long, 3 times the length of the head, distinctly hairy, with 13 flagellomeres, all covered with long setae (shortest 0.02 mm, longest 0.4 mm). Scape broad and short, rounded; pedicel very short. Eye bare, with a distinct dorso-medial extension. Mouthparts lacking functional mandibles; palps long, with 5 palpomeres bearing numerous setae, all approximately the same length. Two postocular setae; frontal, inner vertical and outer vertical setae not visible, possibly absent.

Thorax 0.5 mm long, 0.36 mm wide, 0.1 mm high. Postnotum and scutellum with few, rather short setae. Scutum with a central group of acrostichals and 2 lines of sparse dorsocentrals.



Figs 18–20. *Cretadiamesa arieli* gen. et sp. n., male, holotype 365: (18) general habitus, scale bar = 0.5 mm; (19) wing, scale bar = 0.3 mm; (20) details of male genitalia, scale bar = 0.1 mm.

Wing macropterous, 1.1 mm long, 0.3 mm wide, hyaline, membrane without setae. Costa ending at apex of R_{4+5}, near wing apex. Radius with only 3 branches R_1, R_{2+3}, and R_{4+5}; R_1 rather long, 3 times as long as R_{4+5}; R_{2+3} simple, closely aligned and parallel to R_1 but very weakly indicated; R_1 and R_{4+5} strongly approximate. Cross-vein MCu present in a very basal position, approximately midway between base of M and RM. Fork of Cu nearly opposite RM; Cu_1 weakly curved. Anal vein An_2 absent. Halter 0.18 mm long.

Fore femur length 0.42 mm; mid femur 0.4 mm; tibia 0.6 mm; hind femur 0.48 mm; tibia 0.66 mm. One hind tibial spur visible, curved; hind tibial comb present, disposed in one row.

Abdomen 0.94 mm long, 0.2 mm wide (male); 0.8 mm long, 0.25 mm wide (female). Male genitalia: abdomen with numerous uniform setae; gonocoxite short and broad;

gonostylus directed upward, curved and short, with an apical megaseta; inferior volsella not visible and thus reduced or absent. Female genitalia: tergite IX undivided; cerci short with small setae; gonocoxites IX not visible.

Holotype: 365, male. LEBANON: *Mont Lebanon district* [*Mouhafazit Jabal Loubnan*]: Hammana/Mdeyrij, Caza Baabda; Early Cretaceous (D. Azar coll.).

Allotype: 349, female, same data as holotype.

Discussion: The allocation of the male and female specimens to the same species is based on their similarity in wing venation. Following the key to Holarctic subfamilies of Oliver and Dillon (1989) and to Palaearctic subfamilies in Sæther *et al.* (2000), *Cretadiamesa* gen. n. falls in the Prodiamesinae because of the following characters: macropterous; MCu present; R_{2+3} very weak, but simple; R_1 and R_{4+5} strongly approximate; wing membrane without setae; FCu well distad of MCu. Furthermore, *Cretadiamesa* has bare eyes, unlike in most recent Diamesinae. Among the non-Holarctic subfamilies, affinities with the Aphroteniinae, Usambaromyiinae and Chilenomyiinae are excluded for the same reasons as above. As in *Libanodiamesa, Cretadiamesa* differs from the recent prodiamesine genera in its much more basal position of MCu, midway between base of M and RM.

CONCLUSION

The fossil Chironomidae from the Early Cretaceous Lebanese amber can be attributed to recent subfamilies and, with some uncertainty, to recent tribes. They demonstrate the great antiquity of the chironomid diversity and morphological disparity. Grund (2005) has attempted to use the chironomid subfamily representation in the Cainozoic Dominican amber to infer some palaeoecological data, however he has indicated that such inferences remain speculative. Obviously, there are fewer possibilities to make such inferences for the Early Cretaceous Lebanese amber.

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Two new hymenopteran fossils from the mid-Cretaceous of southern Africa (Hymenoptera: Jurapriidae, Evaniidae)

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ABSTRACT

The deposits at Orapa, Botswana, include several unique specimens of Hymenoptera that provide insights into relationships amongst various higher taxa, and insights into the probable characteristics of their ancestral forms. This paper describes two new monotypic genera and their type species. *Chalscelio orapa* Rasnitsyn & Brothers gen. et sp. n. shows characteristics of Chalcidoidea and Scelionidae, and may be a sister taxon to Chalcidoidea; it is provisionally placed in the family Jurapriidae. *Botsvania cretacea* Rasnitsyn & Brothers gen. et sp. n. shows a mixture of plesiomorphic and apomorphic characters when compared with other species of Evaniidae; its placement at or near the base of Evaniidae is highly probable, but greater certainty requires additional specimens.

KEY WORDS: Hymenoptera, Cretaceous, Gondwana, Botswana, new taxa, wasps.

INTRODUCTION

The lower Upper Cretaceous (Turonian) deposits at Orapa, Botswana, resulted from the kimberlitic eruption that formed a crater about 91 Mya, followed by accumulation of the fossiliferous sediments there (for details see Brothers & Rasnitsyn 2003, and references therein). The Orapa insect fossil assemblage is rich and diverse, currently being the most important source of information about the mid-Cretaceous insect world in the southern hemisphere (reviewed by Brothers & Rasnitsyn 2003). Unfortunately, our knowledge of the Orapa hymenopterans is as yet very poor, being limited, apart from the general review above, to the description of a vespid wasp (Brothers 1992) and some ants (Dlussky *et al.* 2004). The Orapa hymenopteran assemblage includes fossils of primary importance for understanding the higher-level evolution of the order. This paper is devoted to two fossils that provide information on the possible ancestries of the superfamily Chalcidoidea and the family Evaniidae (Evanioidea).

The fossils under study are currently housed in the Bernard Price Institute of Palaeontology (BP) at the University of the Witwatersrand, Johannesburg, South Africa.

TAXONOMY

Superfamily Serphitoidea Brues, 1937

Family Jurapriidae Rasnitsyn, 1983

Genus **Chalscelio** gen. n.

Figs 1, 2

Etymology: The genus name combines the names *Chalcis* and *Scelio*, alluding to the combination of characters both of Chalcidoidea and Scelionidae in the new genus; gender masculine.

Type species: *C. orapa* sp. n., by present designation.

Diagnosis: General appearance as in Scelionidae (Scelioninae), including female antenna clavate with 5 claval segments, geniculate and doubly angled (at apex of scape and before clava), and no anellus apparent; body elongate with long, fusiform, non-petiolate metasoma having 6 apparent segments and no sign of external ovipositor. Forewing venation generally typical of Scelionidae except for angular Cu, and combination of retained M (even if incomplete) and RS apparently lost beyond 2r–rs. Unlike Scelionidae and Platygastroidea in general, but highly reminiscent of Chalcidoidea, pronotum long medially but apparently shortened laterally and possibly not reaching tegula; forewing Cu distinctly angular at fork with M; number of antennal segments (13 evident, but 14 or even 15 possible because of imperfect preservation) low. (Position of antennal attachment (close to clypeus vs. far above it) unknown.)

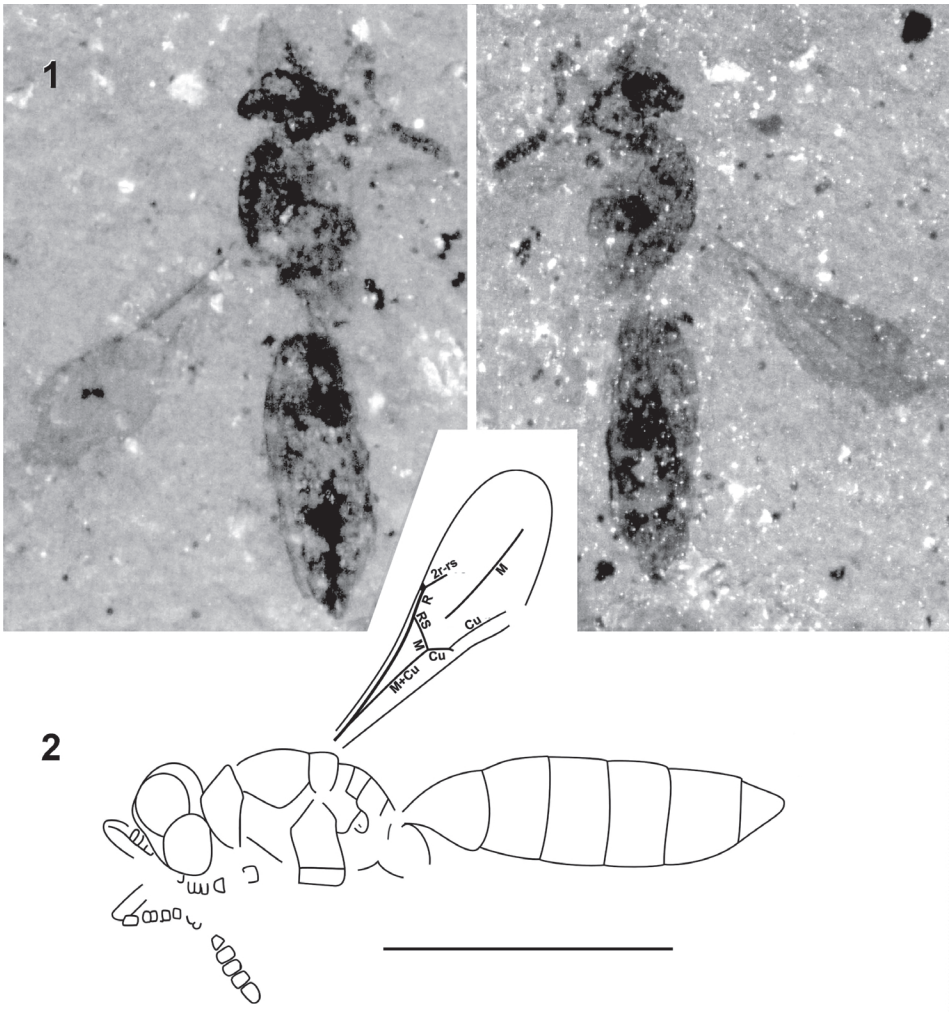
Species included: Type species only.

Phylogenetic position: As far as the characters available permit judgement, the fossil looks essentially like a scelionid, including the double-geniculate antenna, with only three but important anomalous characters, supposedly apomorphies of either Chalcidoidea or (Serphitoidea + Chalcidoidea) as interpreted by Rasnitsyn *et al*. (2004). One of these, putatively synapomorphic for (Serphitoidea + Chalcidoidea), is Cu distinctly bent posteriorly at its junction with M, a state never observed in Platygastroidea or Proctotrupoidea unless combined with cu–a displaced distal of the M+Cu junction (which is not the case here).

Another anomalous character is the medially long pronotum; this state is found in no Platygastroidea and is characteristic of Chalcidoidea. It was probably either independently gained, or independently inherited, by *Chalscelio* and Chalcidoidea directly from the predominantly Jurassic family Mesoserphidae (Rasnitsyn 1980, 1986).

The third character state, the pronotum short enough laterally not to reach the tegula, is tentatively inferred from extrapolation of the direction of the preserved forewing toward the mesosoma. The pronotum does not extend to the tegula in most Chalcidoidea because of the presence of an external prepectus between the two. If the pronotum truly does not reach the tegula in *Chalscelio*, this might imply a large, external prepectus, a feature only of Chalcidoidea. Otherwise, if it is the mesopleuron rather than a prepectus intervening between the pronotum and tegula, this might be a synapomorphy or, more likely, a homoplasy with *Microserphites* Kozlov & Rasnitsyn, 1979 (Serphitidae) and several fossil *Palaeomymar* Meunier, 1901 (Mymarommatidae) (cf. Kozlov & Rasnitsyn 1979, figs 7, 8, 10, 11).

As noted above, *Chalscelio* looks superficially like a female scelionid, notably in having a double-geniculate antenna with 5-segmented clava, apparently only six visible similar metasomal terga and a fusiform metasoma without evidence of an external ovipositor. Of these features, the antennal form is probably the strongest in possibly indicating a close relationship, the other features perhaps likely to be plesiomorphies. However, Rotoitidae, considered a basal lineage of Chalcidoidea, have a 6-segmented clava in the female (5-segmented in the male; other chalcidoids have a clava of three or fewer segments, rarely four; Gibson & Huber 2000), so the claval form in *Chalscelio* does not necessarily indicate a close relationship with Scelionidae. A complication is that Rotoitidae have a scelionid-like pronotum, short medially and reaching the tegula



Figs 1, 2. *Chalscelio orapa* Rasnitsyn & Brothers, gen. et sp. n.: (1) Holotype, BP/2/26990a and b/6, part and counterpart (slightly different scales); (2) Composite drawing; wing veins labelled conventionally. Scale bars = 1 mm.

laterally because the prepectus is linear and concealed under the hind margin of the pronotum, but it is uncertain whether that condition should be regarded as the groundplan for Chalcidoidea. Another complication is that Khutelchalcis Rasnitsyn, Basibuyuk & Quicke, 2004 from the lowermost Cretaceous of Mongolia, another possible basal chalcidoid (Rasnitsyn et al. 2004), shows a different combination of features characteristic of Scelionidae and Chalcidoidea: antenna lacking anelli but apparently with long multiporous plate sensilla and without scelionid-like bend; pronotum short medially and with prepectus not extending far dorsad, but with spiracle accommodated into posterodorsal excision of pronotum; venation essentially scelionid-like whilst metasoma chalcidoid-like (Fig. 3).

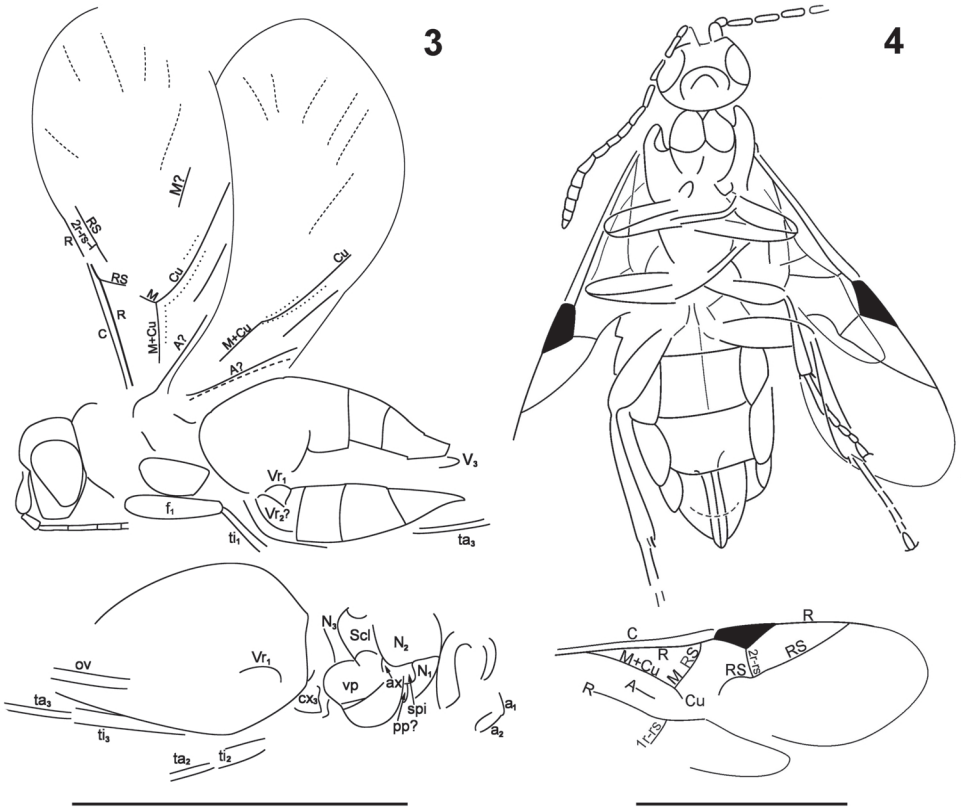
All the evidence taken together makes *Chalscelio* a possible sister group of Chalcidoidea. The basal position of *Chalscelio* with reference to Chalcidoidea is demonstrated by the plesiomorphic (not reduced ring- or tube-like) first metasomal segment, as well as by the wing venation retaining some plesiomorphic details (pterostigma, distal branch of Cu indicating a former connection with A). A sister-group rather than ancestral position is supported by a few venational autapomorphies in *Chalscelio*, such as the loss of RS connected with the 2r–rs crossvein, loss of the anal vein, and possibly loss of the costal vein enclosing the costal space (all of these being present in *Khutelchalcis*). All these autapomorphies are, however, of rather low phylogenetic importance, being common results of miniaturisation (reduction in body size). Numerous phylogenetically important characters (antennal sensilla, position of the mesothoracic spiracle with respect to the pronotum, external vs. internal ovipositor) are not determinable in *Chalscelio* because of the imperfect preservation of the unique fossil. Nevertheless, the available information leads to the conclusion that *Chalscelio* may be morphologically similar to the true chalcidoid ancestor. This characterises the fossil as a relict, because Chalcidoidea are now known from at least the earliest Cretaceous, that is they predate *Chalscelio* by some 40 to 50 million years.

Taxonomic position: This fossil is not a chalcidoid by any current definition, and yet it may be monophyletic with Chalcidoidea. However, to attribute *Chalscelio* formally to Chalcidoidea (naturally as a family of its own) would result in only a single character, the pronotum long medially and shortened laterally, as diagnostic of the resulting assemblage (except for Rotoitidae and Khutelchalcididae). This is impractical, particularly because knowledge of the fossil is incomplete. This is why, until more information is accumulated, we prefer to consider *Chalscelio* formally as a genus of questionable taxonomic position, tentatively grouped together with another such genus, *Jurapria* Rasnitsyn, 1983, for which the family name is already available (Rasnitsyn 1983; Rasnitsyn *et al.* 2004). *Jurapria* differs from *Chalscelio* in the antenna and general appearance, being less strikingly scelionid- or chalcidoid-like (Fig. 4), and in having the wing venation far more complete. Other important characters are hardly comparable because of the different preservation states of the two fossils: the pronotum form is unknown for *Jurapria*, while the position of the ovipositor, short and not tightly enclosed in *Jurapria*, is unknown for *Chalscelio*, although it may be similar or internal (but not long and exerted). The two genera are similar in two other important characters: both are synapomorphic with Serphitoidea + Chalcidoidea in having Cu arching or angular at the fork with M, and both are plesiomorphic with respect to them in having the first metasomal segment not modified into a tube or ring. This provides further justification for the present interpretation of their taxonomic position.

Chalscelio orapa sp. n.

Etymology: The species name, a noun in apposition, is the type locality.

Description: Body length 2.2 mm; forewing length as preserved (wing base perhaps incompletely visible) 1.2 mm. Ground colour moderately dark; head, flagellum, mesopleuron and metasoma darker. No surface sculpture evident. Head transverse, moderately wide (about as wide as mesosoma), with large, almost circular eyes occupying most of the sides. Temples narrow. Position of antennal sockets unknown. Antenna at



Figs 3, 4. (3) *Khutelchalcis gobiensis* Rasnitsyn, Basibuyuk & Quicke, holotype; drawing based on part (above) and counterpart (from Rasnitsyn *et al*. 2004); (4) *Jurapria sibirica* Rasnitsyn, holotype; drawing with fore- and hindwing below (modified after Rasnitsyn 1983). Abbreviations: a_1 – scape, a_2 – pedicel, ax – axilla, cx_3 – hind coxa, f_1 – fore femur, $ta_{2, 3}$ –mid and hind tarsi, $ti_{1–3}$ – fore, mid and hind tibiae, $N_{1–3}$ – pro-, meso- and metanotum (the latter probably with metapostnotum delimited behind), ov – ovipositor, pp? – supposed prepectus, spi – spiracular excision of pronotum, Scl – mesoscutellum, vp – mesothoracic ventropleuron (ventral surface of mesothorax), Vr_1 – supposed upper margin of first valvifer, Vr_2 – second valvifer, V_3 – ovipositor sheath; wing veins labelled conventionally. In wing, dotted line – sharp concave furrow, dashed line – rounded convex fold. Scale bars = 1 mm.

least 13-segmented (number of flagellomeres not precisely known), twice bent (geniculate and bent basal to clava) and clavate. Scape several times longer than wide (full length unknown), wider than flagellum and narrower than clava. Pedicel about as wide as flagellar segments, about one and a half times as long as wide. No true anellar segments evident. Flagellar segments strongly transverse, at least 6 in number, of subequal length and width. Clava 5-segmented, with 1st segment subconical, only slightly wider than flagellar segments; subsequent segments of subequal width and length (except apical segment longer), subquadrangular, about 1.5 times as wide as long; apical segment narrowed toward rounded apex, 1.5 times as long as wide. Mesosoma ovate in dorsolateral view. Pronotum with apparently straight hind margin and weakly defined posterolateral angles. Mesonotum without distinct notauli (possibly because of insufficient preservation). Scutellum apparently wide and short. No distinct axilla evident.

Metanotum ribbon-like, not very short. Propodeum with two transverse lines, with lateral lines (probably incomplete below), and with ovate area surrounding spiracle. Forewing shorter than metasoma, narrow. Costal vein weak or lost. Pterostigma small, almost dot-like. Basal vein weakly oblique, separated from 2r–rs by slightly less than its length; 2r–rs oblique, slightly shorter than its distance from basal vein. No RS present (except for part in basal vein). Distal part of M long, not connected with basal vein. Cu bent posteriorly at fork with M, then bent anteriorly at rudiment of vein formerly closing cell. No trace of cu–a or 1A. Metasoma fusiform, with segment length ratios about 1:0.7:0.7:0.7:0.8:0.5. No external ovipositor evident. Relation between apical tergum and sternum (tightly closing metasomal apex at rest or not) unknown, but at least not wide apart apically.

Holotype: BP/2/26990a and b/6, female (based on form of antenna), almost complete but lacking legs (except for hind coxa) and hind wings. BOTSWANA: Orapa; Upper Cretaceous, Turonian.

Family Evaniidae Latreille, 1802

Genus **Botsvania** gen. n.

Figs 5, 6

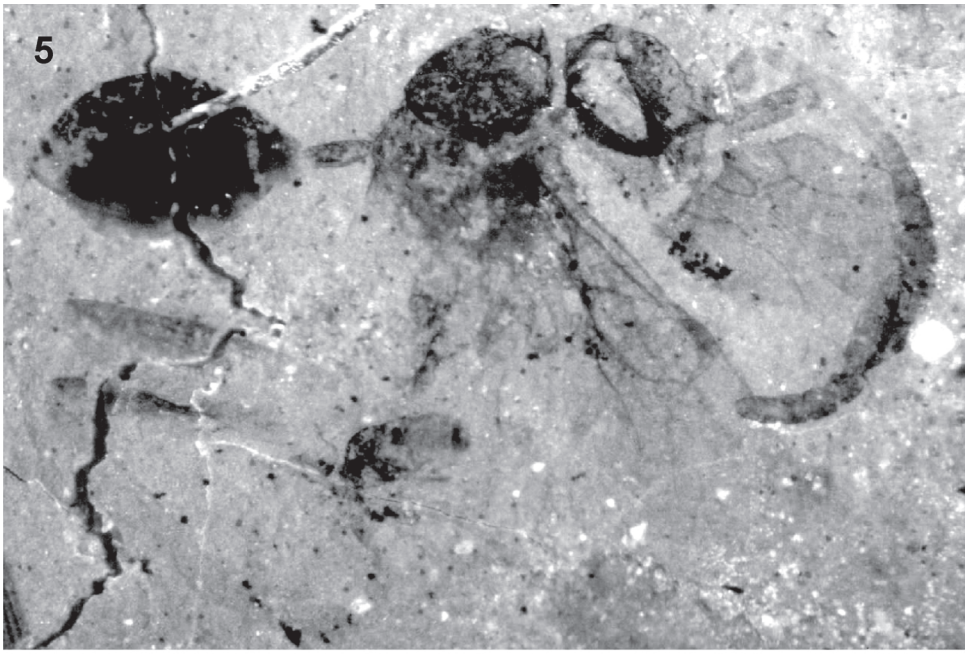
Etymology: The genus name is derived from Botswana and the genus *Evania*; gender feminine.

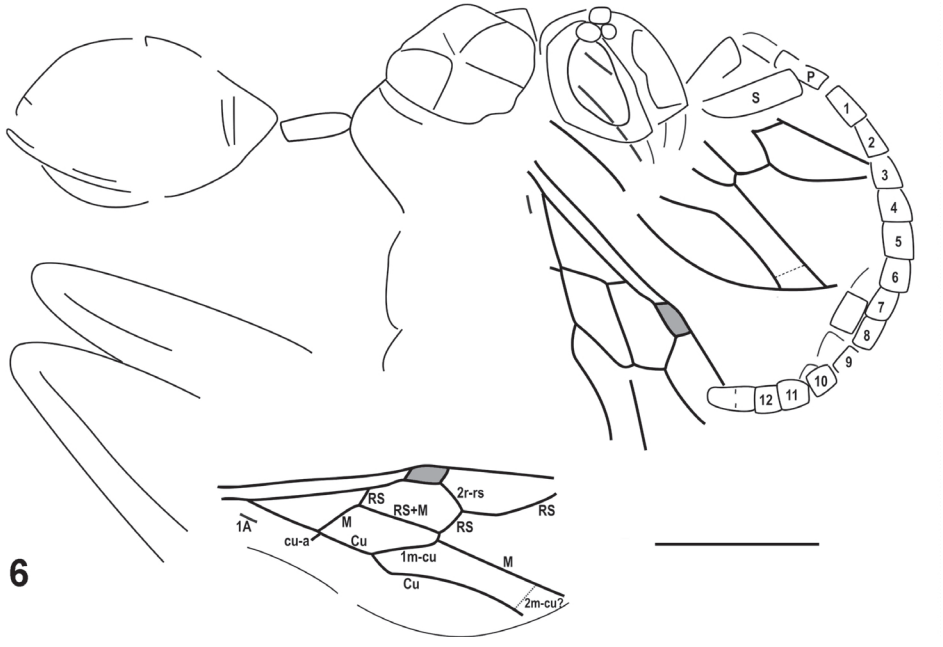
Type species: *B. cretacea* sp. n., by present designation.

Diagnosis: Antenna 15- or 16-segmented, attached near lower orbits. Mesothoracic prescutum and scutellum both triangular; lateral contour of propodeum smoothly rounded, with dorsal surface comparatively long (more than one third as long as posterior surface). Hind leg about as long as in some extant ensign wasps (hind femur as long as head and mesosoma combined). Vein RS+M originating much higher along basal vein than in most other Mesozoic evaniids. Petiolar (1st metasomal) segment subcylindrical, comparatively short and wide (length about 3 times width).

Species included: Type species only.

Taxonomic position: The position of the new genus within Evaniidae is supported by the high attachment of the metasoma on the propodeum (synapomorphy of Evanioidea) combined with the elbowed antenna (unique for Evaniidae in the superfamily), the close association of the head with the mesosoma, the absence of the medial mesoscutal line (present in Praeaulacidae), the position of RS+M well above the mid-height of the basal vein (not above mid-height in Gasteruptiidae s.l.), and the short subcylindrical petiole (conical if modified as a petiole in Gasteruptiidae s.l., long and subcylindrical in Andreneliidae). Within Evaniidae, the new genus combines some outstanding plesiomorphies (lower attachment of antenna, as in Evanioidea other than Evaniidae; triangular prescutum and scutellum, as in Praeaulacidae; and smoothly curved propodeum with comparatively long dorsal surface) with various apomorphies. The antenna with fewer than 25 segments (the number in *Mesevania* Basibuyuk & Rasnitsyn, 2000), the forewing crossveins 2–3r–m and 2m–cu lost as tubular veins, and the short ovipositor suggest monophyly with all evaniids other than *Mesevania*, while the 15- or 16-segmented antenna makes it possibly the sister group of all Evaniidae above *Mesevania* (fewer than 14 segments in all others; Basibuyuk *et al*. 2002, Deans *et al*. 2004). At the same





Figs 5, 6. *Botsvania cretacea* Rasnitsyn & Brothers, gen. et sp. n.: (5) Holotype, BP/2/26835/1; (6) Drawing, with composite forewing below. Antenna: S – scape, P – pedicel, 1–12 – flagellomeres; wing veins labelled conventionally. Scale bar = 1 mm.

time, the high position of RS+M suggests monophyly with higher Evaniidae, that is, with all Cainozoic genera plus the Late Cretaceous (Turonian) *Newjersevania* Basibuyuk, Quicke & Rasnitsyn, 2000. The remaining Cretaceous genera either have RS+M meeting the basal vein near its mid-height (*Mesevania*, *Lebanevania* Basibuyuk, Rasnitsyn, Fitton & Quicke, 2002, *Proparevania* Deans in Deans *et al*. 2004, and Grimaldivania Basibuyuk, Fitton, Rasnitsyn & Quicke, 2000b), or have their wing venation highly modified (the closely related *Cretevania* Rasnitsyn, 1975, *Procretevania* Zhang & Zhang, 2000, and *Eovernevania* Deans in Deans *et al*. 2004 have the basal vein displaced far basad, with the position of RS+M secondarily modified and variable). The comparatively long, narrow, subcylindrical petiole with no apparent borderline between tergum and sternum suggests monophyly with all Evaniidae except *Lebanevania* and *Grimaldivania*, in both of which it is short, stout and conical; the tergum and sternum are clearly delimited in *Lebanevania*. The general habitus with a short body and very long hind legs indicates a synapomorphy with the highest extant evaniids. Thus the phylogenetic indications are strikingly contradictory and might only be balanced by a cladistic analysis. However, the number of characters available is evidently too low to expect any meaningful results from a rigorous cladistic procedure (cf. the results obtained for the better-preserved amber fossils of *Lebanevania* and *Mesevania*; Basibuyuk *et al*. 2002, figs 9–14). Thus we can only conclude that the new genus has an undefined position among the lower (Cretaceous) Evaniidae.

Remarks: *Botsvania* is about coeval with *Grimaldivania* and *Newjersevania* from the Turonian of New Jersey in eastern North America. Those genera are represented by three species, and nothing similar to *Botsvania* has been found there. Similarly, seven other specimens of Evanioidea have been found at Orapa (Brothers & Rasnitsyn 2003), and not one of them is similar to *Grimaldivania* or *Newjersevania*. Also, nothing closely related has been found in numerous Late Cretaceous hymenopteran assemblages of Siberia; Evaniidae are represented there by *Cretevania* (Rasnitsyn, 1980). The older (Hauterivian through Albian) Evaniidae from the Lebanese and Burmese ambers are either unlike or (*Protoparevania*) only superficially similar to *Botsvania* (Basibuyuk *et al*. 2000*a*, 2002; Deans *et al*. 2004). The difference in mean size between impression fossils (from Orapa) and amber inclusions (from New Jersey and many Siberian localities) that often hinder comparison of respective fossil assemblages (Rasnitsyn, 1980), is of less importance in this particular case, because *Newjersevania casei* Basibuyuk, Quicke & Rasnitsyn, 2000 is even larger than *B. cretacea*, and small fossils less than 2 mm long are not uncommon in the Orapa assemblage. This makes it possible to conclude that the Late Cretaceous fauna of Evaniidae was diverse and zoogeographically specific, although not very rich at each particular place.

Botsvania cretacea sp. n.

Etymology: The species name, an adjective, refers to the Cretaceous period.

Description: Length of body 4.2 mm, antenna 3.4 mm, mesosoma 1.3 mm, forewing about 2 mm, hind femur about 2.0–2.2 mm, petiole 0.5 mm, rest of metasoma 1.7 mm. Ocular apodemes, mesonotum and metasoma beyond petiole dark; flagellum beyond 1st segment, head, much of remaining mesosoma, petiole, hind coxa and hind femur,

dorsally, somewhat darkened; otherwise pale. No surface sculpture evident. Head with eyes large and elongate, occupying most of sides, with almost straight inner and convex outer orbits; ocelli large (indicating crepuscular to nocturnal activity). Mouthparts scarcely distinguishable. Antenna as long as meso- and metasoma combined, with scape almost 0.7 times as long as head capsule, about 3.5 times as long as wide, parallel-sided except narrowed basally over 0.3 of ventral contour. Pedicel narrower than scape, subcylindrical, about 1.5 times as long as wide. Flagellum 13- or 14- segmented (subdivision of apical segment not distinct), widest at and beyond middle, with segments gradually shortening toward apex, with 1st flagellomere twice as long as wide and 12th slightly transverse; apparently apical segment again twice as long as wide (if really double, true subapical segment distinctly transverse and true apical segment slightly longer than wide, narrowed toward rounded apex). Pronotum only partially preserved, apparently with straight anterior and deeply emarginate posterior margins, very short medially. Mesonotum almost symmetrical with respect to transscutal suture, with scutum between notauli and scutellum mirroring each other. Metanotum short, ribbon-like. Propodeum with declivity almost straight, about 2.5 times as long as horizontal surface (disc); junction of disc and declivity rounded. Hind coxa in-completely preserved, apparently elongate, not much shorter than height of pro-podeum. Hind femur and tibia long and narrow, femur about as long as metasoma, tibia apparently lacking irregular apical thickening (as described for *Mesevania*). No other leg parts preserved. Pterostigma fairly small, almost parallel-sided, with short oblique apex, 2r–rs originating near pterostigmal apex. Basal vein separated from pterostigma by about pterostigmal length, with RS forming less than its upper one-third. RS+M parallel to Cu (not to 2r–rs, as in many advanced Evaniidae); 2r–rs longer than abscissa of RS between it and RS+M (unlike in most Mesozoic Evaniidae except *Mesevania*). No rs–m crossveins present as tubular or nebulous veins. M meeting 1m–cu shortly after leaving RS+M (unlike in *Mesevania, Lebanevania*, and *Grimaldivania*); 1m–cu oblique, 2m–cu possibly present as weak nebulous vein placed near apical wing margin. Cu characteristically bent shortly beyond 1m–cu, but with no sign of connection to 1A there. Crossvein cu–a preserved as short stub just distal to M+Cu fork. Short section of 1A seen near wing base only. No hind wing apparent. Petiole with no apparent boundary between tergal and sternal parts, subcylindrical except narrowed basally over anterior quarter, 3 times as long as wide, as long as scutum. Rest of metasoma broadly fusiform, unknown if compressed, with basal segment almost triangular in lateral view, otherwise segmentation not evident. Ovipositor as preserved not extending beyond metasomal apex, slightly bent upward.

Holotype: BP/2/26835/1, female, almost complete fossil but lacking lower mesosoma, fore and mid legs and hind wings. BOTSWANA: Orapa; Upper Cretaceous, Turonian.

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Rooting the phylogenetic tree for winged insects: independent adaptations to terrestrial life

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ABSTRACT

Although numerous articles have been published on insect phylogeny using a great variety of techniques, there is no consensus on the nature of the first winged insects, the ancestors of holometabolous insects or the causes for the origin of metamorphosis. This discord has resulted in the lack of secure foundations within entomological theory. However, several recent articles provide key information which may help to resolve some of the long-standing disputes. Some biologists have argued that the first winged insects might have been amphibiotic rather than terrestrial and that metamorphosis might have originated as an adaptation to amphibiotic life. Thus entomological theory may now be passing through a paradigm shift where, for the first time, the phylogenetic tree for all insects may be firmly rooted.

KEY WORDS: Adaptation, ancestors, aquatic, entomology, insect, metamorphosis, paradigms, phylogeny, terrestrial, wings.

INTRODUCTION

Ideas about the origin and evolution of insects can be traced back to Aristotle, but entomologists still do not understand the interrelationships of insect orders and have not reached consensus on the origin and appearance of the first holometabolans (Bitsch *et al.* 2004). One of the greatest controversies in entomology concerns the rooting of the phylogenetic tree for winged insects, and the stems of the different orders. Without knowledge of the ground plan of a taxon there is no basis for objective comparison with other taxa (Willmann 1997). Although DNA sequence data are now available from most major insect orders (Giribet & Ribera 2000; Whiting 2002; Bitsch *et al.* 2004), there has been a lack of coordination of studies and it has been said that the whole of our efforts is little greater than the sum of its parts (Caterino *et al.* 2000). Although cladistics or phylogenetic systematics has helped to sort out many relationships, it also has inherent limitations and is not capable of resolving ancestor-descendant relationships because these appear as sister groups that originated simultaneously (Krell & Cranston 2004). This suggests that Lepidoptera and Trichoptera are equally ancient, even though Trichoptera are known from much earlier in the fossil record (Carpenter 1992). This leads to the conclusion that there is a hypothetical gap in the fossil record of Lepidoptera (Toms 1985). If Lepidoptera and Trichoptera are seen as sister groups, this presupposes a concept of evolution and it is therefore reasonable to investigate the nature of the hypothetical ancestor of each group. Ultimately, there should be agreement between morphology, molecular phylogenetics, developmental biology and theoretical biology. Unfortunately, the hypothetico-deductive method has not been fully utilized, and thus key issues have been ignored. For example, theoretical entomology suggests that the amphibiotic orders Ephemeroptera, Odonata, Plecoptera, Megaloptera and Trichoptera may be critical orders in the evolution of insects, yet they have been omitted from many molecular studies (e.g. Caterino *et al.* 2000).

Most hypotheses about the origin and evolution of insects can be accommodated in one of two opposing models (Table 1), an aquatic model (Toms 1984*a*, 1986) or a terrestrial model (Little 1990; Pritchard *et al.* 1993). A compromise between these models has also been proposed (e.g. Kukalová-Peck 1978). A solution to this dispute could have a dramatic impact on entomological theory, especially if it is resolved in favour of the aquatic model, as the terrestrial model has been considered as one of the dominant paradigms of the last century.

The choice of a root has profound effects on the major branches of the phylogenetic tree. In the terrestrial model, the ancestors may have resembled cockroaches which are known to exist early in the fossil record (Carpenter 1992). The choice of a terrestrial candidate for the ancestor of all winged insects is a matter which needs to be resolved by those who support the terrestrial model. This insect may have played a crucial role in the evolution of winged insects. In the terrestrial model it is accepted that all aquatic insects are secondarily aquatic. If this is the case, numerous independent adaptations to aquatic life occurred. Although the terrestrial model received the majority of support in the last century, and most research has been channelled in this direction (Little 1990; Truman & Riddiford 1999), progress in substantiating such a theory has been disappointing. In fact, Caterino *et al.* referred to the state of insect molecular systematics in 2000 as a 'thriving Tower of Babel'. Since then, some progress has been made (Wheeler *et al.* 2001; Bitsch *et al*. 2004), but there is still no generally accepted hypothetical (or real) ancestor for the winged insects or the holometabolous insects, and no generally accepted explanation for the origin of wings and metamorphosis.

In contrast, according to the aquatic model, the ancestors of insects were Crustacea (Hansen 1893; Crampton 1918; Regier & Shultz 1997; Shcherbakov 1999) and the ancestors of winged insects resembled primitive mayfly larvae (Gegenbaur 1874; Toms 1984*a*). According to this model the ancestors of winged insects were aquatic and the first winged insects were amphibiotic, with aquatic larvae and terrestrial adult stages. In the aquatic model, metamorphosis originated as an inevitable consequence of an amphibiotic life cycle, with the adults adapting to terrestrial life while the larvae remained aquatic. In amphibiotic insects such as Odonata or Ephemeroptera, the aquatic larval stages and terrestrial adults are different and the changes occur with a change in habitat at metamorphosis. It is thought that an aquatic life-style was an initial characteristic of larvae of the amphibiotic orders Ephemeroptera, Odonata, Plecoptera, Megaloptera and Trichoptera. Accordingly, the larval stages of insects became terrestrial independently on several occasions. The most important plesiomorphic characters are those relating to the aquatic life of the juvenile stages, and some of the major branches of the phylogenetic tree should comprise the primitive amphibiotic orders. Many important apomorphic characters are associated with adaptations to terrestrial life in larvae. Despite these considerations, the aquatic model has not been fully explored. Nevertheless, a great deal of progress has been made recently and we may now be moving towards a paradigm shift where the phylogenetic tree for all insects could be firmly rooted for the first time.

Another possibility is a compromise between the aquatic and terrestrial models as suggested by Kukalová-Peck (1978). Starting from a distant aquatic ancestor (all terrestrial arthropods must have evolved from an aquatic ancestor at some time), it is suggested that the ancestors of winged insects left the water and then returned to water

TABLE 1
Some of the major differences between the Aquatic Model and the Terrestrial Model presented. approximately in chronological order.

The Aquatic Model	The Terrestrial Model
Insect ancestors were aquatic, related to primitive Crustacea.	Insect ancestors were terrestrial, related to primitive Myriapoda.
Ancestors of winged insects (Pterygota) were aquatic and resembled Ephemeroptera (mayfly) larvae.	Ancestors of Pterygota were terrestrial and resembled Zygentoma (silverfish).
The first Pterygota were amphibiotic, with aquatic larvae and terrestrial adults.	The first Pterygota were terrestrial in all life stages.
Arthropod tracheal respiratory systems developed several times. In early Pterygota they developed in the terrestrial adult stage.	Tracheal respiratory systems of all insects were derived from unknown terrestrial arthropod ancestors.
Wings are equivalent to gills of mayfly larvae, and evolved from existing ancient organs that can be traced back to Crustacea.	Insect wings are new developments which originated as paranotal lobes and were first used for gliding.
Holometabolous larval legs and prolegs had a common origin with the legs of adult insects.	Holometabolous larval legs and prolegs are new developments and are not equivalent to adult legs.
The most primitive living Pterygota are Ephemeroptera.	The most primitive living Pterygota may be Blattodea.
Metamorphosis originated as an inevitable adaptation to an amphibiotic life style.	Metamorphosis originated in a terrestrial hemimetabolan or early holometabolan as an adaptation enabling resource partitioning.
Terrestrial hemimetabolous insects such as Blattodea, Orthoptera and Hemiptera evolved from amphibiotic ancestors like Ephemeroptera and Plecoptera.	Amphibiotic orders such as Ephemeroptera, Odonata and Plecoptera evolved from terrestrial ancestors like Blattodea.
Amphibiotic holometabolous insects such as Megaloptera and Trichoptera evolved from amphibiotic ancestors, which may or may not have been hemimetabolous.	Amphibiotic holometabolous insects such as Megaloptera and Trichoptera evolved from terrestrial holometabolous insects.
Terrestrial holometabolous insects such as Coleoptera, Lepidoptera and Diptera evolved from amphibiotic holometabolous insects such as Megaloptera and Trichoptera.	Terrestrial holometabolous insects evolved from terrestrial hemimetabolous insects and the aquatic larvae of Megaloptera and Trichoptera are secondarily aquatic.

again to give rise to Ephemeroptera, Odonata and Plecoptera. Once this had occured, complete metamorphosis could have originated in amphibiotic insects, as suggested in the aquatic model. Eventually it may be necessary to accept that the ancestors of Ephemeroptera were terrestrial, but there is still no compelling evidence for this entirely hypothetical terrestrial stage (Sinitshenkova 2002; Zherikhin 2002). Ephemeroptera are the most primitive winged insects (Engel & Grimaldi 2004), but all living examples have aquatic larvae and there is no evidence that the first Ephemeroptera had terrestrial larvae. Before metamorphosis evolved, one set of genes presumably determined the morphology of the larvae and the adults, so both aquatic and terrestrial stages of an amphibiotic insect would have been adversely affected by this limitation until metamorphosis and/or phase-specific genes evolved (Toms 1984*b*). The recently discovered oldest mandible of a winged insect may suggest that the winged insects are 80 million years older than previously thought (Engel & Grimaldi 2004), which would mean that winged adult insects existed about 400 million years ago. However, this does

not indicate that these winged insects had terrestrial larvae or not. The concept of an earlier origin of insects at a time when the terrestrial environment was generally hostile with little vegetation, would indicate that the fossil record is far less complete than previously imagined. The hypothesis that metamorphosis evolved in amphibiotic ancestors of the winged insects is not significantly affected by any evidence for or against a hypothetical terrestrial stage ancestral to Ephemeroptera. Such a hypothesis is not considered within this paper since the explanation of metamorphosis is the same as in the aquatic model. The aquatic model provides potential answers to problems which are not explained in the terrestrial model, so it needs to be examined carefully before we accept an extra hypothetical stage in the evolution of the winged insects.

DISCUSSION

Independent adaptations to terrestrial or aquatic life?

Generally, there is agreement that insects have crossed environmental barriers from aquatic to terrestrial life or *vice versa* on numerous occasions, whether we follow an aquatic model or a terrestrial model for the evolution of insects. When an environmental barrier is crossed, such as from aquatic to terrestrial life, major adaptations have to occur. Such a transition would affect the digestive, respiratory, locomotory and circulatory systems, in addition to vision, which would all have to be significantly modified in order to allow for life within a terrestrial environment (Toms 1984*a*; Little 1990). One of the most important changes is the development of the respiratory system and this has been seen as a difficulty for the aquatic model. However, it has been suggested that the tracheal respiratory system first evolved in ancestral insects, which began to leave water for part of their life. Tracheae developed in the adult stages and their branches subsequently ramified into abdominal appendages of aquatic immatures (Riek 1971). When an environmental barrier is crossed several times in the same direction, we should find evidence of independent adaptations to the new environment, and several possible test cases have already been identified and discussed (Toms 1984*a*, 1986). Although the terrestrial model suggests that insects moved from land to fresh water on many occasions, a process which was well understood by Miall in 1895, they surprisingly seldom colonised the marine environment. In contrast, the aquatic model suggests that winged insects originated in fresh water and became terrestrial a few times, the paucity of marine insects is thus less surprising. According to both models, many habitat changes occurred in both directions providing us with an opportunity to investigate the direction of evolution and finding a way of rooting the phylogenetic tree.

Recent developments

Recent evidence shows that there are more similarities between ribosomal and mitochondrial DNA of insects and crustaceans than between insects and myriapods (Regier & Shultz 1997; Boore *et al.* 1995; Friedrich & Tautz 1995; Cameron *et al.* 2004), indicating that Myriapoda and Insecta are probably not monophyletic as was commonly assumed (Little 1990). The remarkable similarity in the construction of the brains of insects and crustaceans supports this conclusion (Osorio *et al.* 1995). This means that one of the most important assumptions which supports the theory that insects

evolved from terrestrial myriapods is no longer valid and that they might have actually arisen from some ancestral aquatic Crustacea. Averof and Cohen (1997) found that homeobox genes expressed in fruit fly (*Drosophila*) wings are also expressed in crustacean exopodites or gills, suggesting that wings may be ancient appendages dating back to Crustacea, and not relatively 'recent' novelties. This discovery is significant, since it contradicts the paranotal-lobe theory for the origin of insect wings in silverfish-like ancestors and thus excludes Zygentoma as plausible ancestors of winged insects (Quartau 1985; Hasenfuss 2002). Since the hypothesis that wings are new developments has been discredited (Averof & Cohen 1997), it is proposed that the ancestors of winged insects must have had appendages from which wings could have evolved, and may have resembled primitive mayfly larvae (Kukalová-Peck 1985; Marden & Kramer 1994; Will 1995).

Ancestors of holometabolous insects

The origin of holometabolous insects is one of the key events in the evolution of winged insects. Traditional classifications assume that Holometabola are monophyletic and that their undisclosed ancestor was terrestrial (Hennig 1981). However, in the aquatic model, terrestrial holometabolous larvae may be polyphyletic. The most probable ancestral groups are Ephemeroptera, Plecoptera, Megaloptera, Trichoptera and amphibiotic Mecoptera, and the most important primitive characteristic is an aquatic life-style of their larvae.

Although several molecular phylogenies have appeared (e.g. Giribet & Ribera 2000; Wheeler *et al.* 2001; Whiting 2002; Bitsch *et al*. 2004), there is no clear evidence that terrestrial orders are primitive and there is a lack of plausible ancestors for the amphibiotic orders. Recent evidence from ribosomal DNA consistently points to a close relationship between Trichoptera and Lepidoptera (Giribet & Ribera 2000), but the larvae of Trichoptera are aquatic while those of Lepidoptera are generally terrestrial and those species with aquatic larvae are relatively specialised. The close relationship between Trichoptera and Lepidoptera is generally accepted, but the primitive state of the larvae (aquatic or terrestrial) is controversial (Hennig 1981). The egg, larva and pupal stages of the life cycle of Trichoptera are all aquatic and the adults re-enter the water to lay eggs (Morse 1997), suggesting that aquatic larvae may be primitive. Significantly, new evidence from ribosomal DNA suggests that Trichoptera consistently form a lower branch in the clade composed of Lepidoptera and Trichoptera (Giribet & Ribera 2000), pointing towards an aquatic habitat for the ancestral larvae. A similar situation exists in the case of Megaloptera (Haring & Aspöck 2004), where Megaloptera appear to be more primitive than Neuroptera and have aquatic larvae. In the aquatic model, it may be suggested that the origin of a terrestrial lifestyle in the larval stages was a major event in the origin of Neuroptera (Aspöck 2002).

Evolution of insect eyes

Another relevant development is a review of information concerning the structure of the eyes (stemmata) of holometabolous larvae (Gilbert 1994). Gilbert found that in comparison to the eyes of hemimetabolous nymphs that are similar to those of the adults, eyes of holometabolous larvae are highly reduced and very different from those

of the adults. The only holometabolous larvae with vestigial compound eyes are Mecoptera (Gilbert 1994), notably the aquatic larvae of Nannochoristidae (Byers & Thornhill 1983). The Nannochoristidae have a suite of characters that are presumably primitive for Mecoptera and occupy the basal branch in Mecoptera phylogeny (Willmann 1987), and there is a trend towards the reduction of eyes from primitive aquatic species to advanced terrestrial species, as in other holometabolous larvae. In the aquatic model, the reduction in size of larval eyes could have arisen as a consequence of aquatic larval life, where the visual requirements in aquatic larvae were different from those of the terrestrial adults. The original reduction of larval eyes of holometabolous larvae must have occurred very early in their evolution, coinciding with the origin of metamorphosis, at a time when adaptation to different environments was prevalent at different stages within an amphibiotic life cycle (Toms 1984*b*). In Coleoptera, Crowson (1981) argued that reduction in numbers of stemmata from the maximum number of seven pairs (also found in some Mecoptera) is an irreversible evolutionary event, and that the number of stemmata is a good phylogenetic character since it is consistent with our understanding of Coleoptera phylogeny. It appears that Crowson's rule regarding reduction in stemmatal number may be true for all holometabolous insects if the aquatic model is valid. However, in the terrestrial model, one would have to suggest a reason for reduction of stemmata in terrestrial larvae and a reversal or increase in the number of stemmata in aquatic larvae. For example, referring to Gilbert (1994), aquatic megalopteran larvae typically have seven pairs of stemmata while most terrestrial larvae have fewer. Although neuropteran larvae primitively possess seven pairs of stemmata, the most ventral stemma is reduced in all taxa examined. In Coleoptera, the maximum number of six pairs is found in primitive aquatic adephagous larvae, while in Diptera the primitive number of stemmata (found in aquatic Nematocera larvae) is five pairs. Most of the primitive flies (Nematocera) have aquatic or semiaquatic larvae (Yeates & Wiegmann 1999), and this needs to be explained, together with the evolution of the unique respiratory systems of Diptera larvae (Clarke 1979). Such systems can be seen to reflect important apomorphic characters that may have originated as an adaptation to life in anaerobic water, allowing aquatic larvae to breathe air. In the aquatic model, the possibility that primitive Nematocera remained aquatic but developed the ability to breathe gaseous oxygen is congruent with the apparent trend from wet to drier habitats (such as fruit and dung) in fly larvae. If Diptera larvae developed the ability to breathe gaseous oxygen independently of other orders we would expect to find additional independent adaptations to terrestrial life, such as alterations in blood physiology. In fact, Diptera may have a strong dependence on Na^+ rather than Cl^- ions in their haemolymph unlike other aquatic insects where the reverse is often true (Sutcliffe 1963).

The basic number of seven pairs of lenseless stemmata is also found in Trichoptera larvae (Gilbert 1994), and these amphibiotic insects, together with Megaloptera, are regarded as primitive holometabolans within the aquatic model. In the terrestrial model, it has been seen as an anomaly that Trichoptera larvae are aquatic (specialised), while in other ways Trichoptera are more primitive than Lepidoptera (Hennig 1981). If aquatic Trichoptera larvae are advanced, it is also an anomaly that some of them have the primitive number of seven pairs of stemmata. Larvae in the primitive lepidopteran family Agathiphagidae also have seven pairs of stemmata, but in the Micropterygidae, which

are sometimes regarded as the most primitive family in the terrestrial model, there are only five pairs of stemmata (most Lepidoptera larvae have six pairs of stemmata).

Testing the models

Differences in interpretation of the aquatic and terrestrial models require that tests be set up in order to refute one of the models. If aquatic insects are more primitive, the most parsimonious phylogenetic tree would have an aquatic stem with amphibiotic orders forming the basal branches from which terrestrial orders evolved. In contrast, a terrestrial model predicts that we should find a terrestrial stem with both terrestrial and aquatic branches. Terrestrial models that date back to Aristotle have failed to provide a framework capable of making verifiable predictions, and many anomalies exist. However, many observations that seem odd in the terrestrial model are anticipated in the aquatic model, which also suggests solutions to problems. For example, the difficulties experienced in explaining the origin of Hymenoptera may be a consequence of the larval stage of this group moving from aquatic to terrestrial life, which could have affected the morphology of the adult because they share the same genes. Lepidoptera may be viewed as Trichoptera with terrestrial larvae and the adaptation to terrestrial life is likely to have provided the driving force for the evolution of lungs in Lepidoptera larvae (Locke 1998) as well as a wide array of hexamerines in their highly developed haemolymph (Sutcliffe 1963; Telfer & Kunkel 1991). An interesting finding from ribosomal DNA, is that grasshoppers and crickets consistently resolve in different clades (Giribet & Ribera 2000), suggesting that the division between them is ancient and more significant than that between, for example, Trichoptera and Lepidoptera. This indicates that Kevan (1986) may have been correct in suggesting that the suborders Caelifera (grasshoppers) and Ensifera (crickets, katydids etc.) should be regarded as different orders because there are many differences between them and no shared apomorphies. Jumping legs may have evolved independently in Caelifera and Ensifera, as a result of adaptation to terrestrial life in the larval stages.

CONCLUSION

By focussing on major differences in the aquatic and terrestrial models, it should be possible to refute one of the models, establish a secure root for the insect phylogenetic tree and resolve most of the basic interrelationships between the different orders. It is a pity that data on the most interesting insects from a phylogenetic point of view, such as Megaloptera and Trichoptera, has seldom been collected. This would not have occurred if due attention had been given to the alternative predictions of the aquatic model. If evolutionary theory is used to make testable hypotheses and more attention is paid to problem solving, this will dramatically increase the rate at which progress is made.

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A reassessment of the Cretaceous amber deposits from France and their palaeontological significance

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ABSTRACT

The Cretaceous amber deposits from France are reviewed, and their palaeontological content is discussed in the light of recent studies. Numerous "old" amber localities mentioned at the beginning of the 20th century or studied during the 1970s are no longer accessible, but recent field investigations have led to the discovery of new deposits. Among these, the Late Albian amber from Charente-Maritime (SW France) is particularly rich in biological inclusions and thus constitutes one of the major fossiliferous amber deposits for the Cretaceous period. Without having all groups studied, the authors made significant new records and identified taxa occuring in this French amber. This contributes to an improvement of our current knowledge on the evolution and diversity of Mesozoic insects.

KEY WORDS: Amber, Cretaceous, France, arthropods, insects, assemblages, inclusions.

INTRODUCTION

Studies of the Cretaceous amber of France started at the beginning of the 20th century when Lacroix (1910) described the physical and chemical properties of what he named "retinites", and listed approximately fifty deposits of Cretaceous fossil resins. Among these, he cited the presence of an abundant yellow opaque resin in the Cenomanian lignitic clay from two north-western regions (Sarthe and Maine-et-Loire) and from Enet Island (Charente-Maritime, SW France) (Fig. 1). He considered this latter locality as the most important French deposit of fossil resin, together with that of Saint-Lon in Landes (Fig. 1). From various sites Lacroix collected numerous samples which were deposited in the Muséum national d'Histoire Naturelle (MNHN) in Paris. Further chemical analyses were launched between 1963 and 1978, mainly on Cretaceous resins from Sarthe and Charente-Maritime (Chauffin 1963; Schlüter 1978; Savkevitch & Popkova 1978). Based on infrared spectroscopy, the latter placed these resins close to valchovite, a Russian variety of fossil resin (Savkevitch 1974). Some amber pieces collected by Schlüter, but of unknown provenance (probably Bezonnais in Sarthe, Lambert, pers. comm.), were later used for a Nuclear Magnetic Resonance characterisation of Cretaceous amber (Lambert *et al.* 1996; Lambert & Poinar 2002) and were ranged within the group of *Agathis*-like resins.

Galippe (1920) first studied the micro-organisms of amber from Briollay (Maine-et-Loire), but detailed examinations for fossiliferous content were attempted only in the 1970s with Cenomanian ambers from north-western France. Indeed, Kühne *et al.* (1973) described a micropterygid lepidopteran from Bezonnais, and Schlüter (1978) recorded Ascomycetes and 71 fossil arthropods, mainly insects, from Bezonnais and Durtal. He described or figured 34 species in 13 insect families and 5 specimens in Arachnida (Table 1). He also analysed some amber pieces from the Lower Cenomanian of the

Fig. 1. Geographical location and age of the Cretaceous amber deposits of France. Squares correspond to localities previously studied but no longer available in 2005, circles mark the outcrops which are currently visible: (1) Ecommoy (Bezonnais); (2) Durtal; (3) Briollay; (4) Aix Island; (5, 6) Fouras Peninsula: (5) Enet Island, (6) Fouras/Bois-Vert; (7) Tonnay-Charente (Les Renardières); (8) Archingeay-Les Nouillers; (9) Cadeuil; (10) Champniers (La Buzinie); (11) St-Lon; (12) St-Cyprien; (13) Fourtou; (14) St-Marcel-de-Carreiret; (15) Piolenc; (16) Salignac; (17) Belcodène.

Fouras Peninsula and Aix Island in Charente-Maritime, but without any discovery of fossil inclusions. Later, Matile (1981), Schlüter and Stürmer (1982), Schlüter (1983, 1989) and then Szadziewski and Schlüter (1992) gave further details and new descriptions for this entomofauna (Table 1).

Waggoner (1994) described an aquatic micro-assemblage of bacteria, fungi and protists from the Cenomanian amber of Bretagnolles (Eure). However, this provenance seems to be erroneous and the amber is likely to have originated from Bezonnais where similar micro-organisms were recently described (Breton & Tostain 2005).

Thus, previous studies of the French Cretaceous amber focused mainly on the Cenomanian deposits of Bezonnais and Durtal (NW France), and almost all studies were based on chemical analyses, which established an araucarian origin for the amber. Curiously, studies of the fossiliferous content were rather scarce, and less than one hundred inclusions were recorded in 12 arthropod orders.

TABLE 1

List of inclusions previously mentioned from the Cretaceous (Cenomanian) amber of France.

Group	Family	Taxon	Provenance
Arachnida			
Opilionida		sp. A [b]	Bezonnais
Acari		sp. A, B [b]	-
Araneae		sp. A, B [b]	-
Insecta			
Blattodea		sp. A [b]	-
Isoptera		*Lutetiatermes prisca* [a]	-
		Mastotermes sarthensis [a]	-
		sp. C, D, E, F, G [b]	-
Psocoptera		sp. A [b]	-
Heteroptera		sp. A [b]	-
Neuroptera	Rhachiberothidae	*Retinoberotha stuermeri* [b]	-
Coleoptera	Staphylinidae	*Stenus inexpectatus* [b]	-
		Staphylininae sp. A [b]	-
Lepidoptera	Micropterygidae	sp. A [c]	Durtal
Hymenoptera	Mymaridae	*Galloromma bezonnaisensis* [b]	Bezonnais
	Scelionidae	*Cenomanoscelio pulcher* [b]	-
		sp. A, B, C [b]	-
	Sphecidae	*Gallosphex cretaceus* [b]	-
	Diapriidae	Ismarinae indet. [b]	-
	Falsiformicidae	sp. A [b]	-
	Fam. indet.	sp. A, B, C [b]	-
Diptera	Empididae	*Ecommocydromia difficilis* [b]	-
	Limoniidae	sp. A [b]	-
	Ceratopogonidae	*Atriculicoides cenomanensis* [d]	Durtal
		Atriculicoides incompletus [d]	-
		Austroconops borkenti [d]	Bezonnais
		Leptoconops [d]	-
	Cecidomyiidae	sp. A [b]	Durtal
	Keroplatidae	*Schlueterimyia cenomanica* [e]	Bezonnais
	Nematocera indet.	sp. A [b]	-

TOTAL, described or figured arthropods: 39; TOTAL, mentioned inclusions: 71

[a] Schlüter 1989; [b] Schlüter 1978; [c] Kühne *et al.* 1973; [d] Szadziewski & Schlüter 1992; [e] Matile 1981.

MATERIAL

In a general conspectus of all the French ambers, Nel *et al.* (2004*a*) mentioned 55 Cretaceous localities (12 Albian, 32 Cenomanian, 2 Turonian, 3 Santonian, and 6 Maastrichtian). This included some newly discovered localities as well as those previously listed in the literature (Lacroix 1910; Schlüter 1978), but lacked any detail with regard to their present availability. Here we present the state of the art in our investigations launched since 1999 in order to recover the 'historical' localities as well as to discover new deposits. Twelve outcrops are currently available for excavation of amber (Fig. 1), among which ten are fossiliferous. Their ages and a list of their biological content are presented and discussed below. The preliminary analyses of three of them, previously presented by Néraudeau *et al.* (2002, 2003, 2005) and Perrichot (2004), are also completed. Material from the "old" localities studied by Schlüter is held in the Institut für Paläontologie, Museum für Naturkunde, Berlin, Germany. The material from all other studies is held in the Laboratoire de Paléontologie, Muséum national d'Histoire Naturelle, Paris, France. The discussion below only deals with personal data on the latter material, data on faunal assemblages from "old" localities being used for comparison in the conclusion section.

RESULTS

The rich amber-bearing Cenomanian strata of Bezonnais and Durtal (NW France, Sarthe and Maine-et-Loire) were located in quarries which do not exist today. However, an old quarry still exists close to Durtal (e.g., Briollay), which provided a few amber fragments without any inclusions. We failed to find new available outcrop in these regions. Investigations into the mid-Cretaceous amber of northern France have also failed, although Albian and Cenomanian strata containing numerous fragments of lignitic wood are still exposed on the cliffs of the Seine-Maritime region. Lastly, we were unable to locate the presumably rich (Lacroix 1910) amber-bearing deposits of Enet Island and St-Lon (Aquitain basin), as well as those mentioned around St-Cyprien in the Sarladais (Lacroix 1910; Colin 1973), due to the current bad condition of the outcrops.

In south-eastern France, five deposits currently yield a small amount of amber. Cenomanian deposits at Fourtou and Salignac (Fig. 1: localities 13 and 16) provide dark red-coloured nodules ranging from 5 to 30 mm and representing fragmented flows, in which about 30 and 15 arthropods have been found respectively (Table 2). In the three other deposits of Turonian and Santonian age (Fig. 1: localities 14, 15 and 17), most of the amber pieces are translucent light yellow to red-coloured marbles ranging from 3 to 10 mm in diameter. From these, fossil insects have been detected only in the Santonian amber of Piolenc and Belcodène (Table 2).

Finally, six amber deposits of both Albian and Cenomanian age have been accessible in Charente-Maritime and Charente departments in the last five years (Fig. 1: localities 4, 6–10), including those of Fouras Peninsula and Aix Island which were previously studied by Schlüter (1978). Analyses have revealed biological inclusions in all of the six amber deposits, although only the locality of Archingeay-Les Nouillers is highly fossiliferous (Table 2). Indeed, this is the most fossiliferous amber deposit thus far for the Cretaceous of France and the second richest among all French ambers after that of the Eocene of Oise (Nel *et al.* 2004*a*). The five other deposits have provided fewer inclusions since they were either discovered more recently and need further analyses (quarry of Cadeuil and trench of motorway works in La Buzinie at Champniers), or the outcrops are less or no longer accessible in 2005 and thus provided a smaller amount of material (Fouras Peninsula and Aix Island cliffs, and quarry of Les Renardières at Tonnay-Charente). Amber from the six localities presents similar properties and is thought to be mainly of araucarian origin, although other conifers of the families Cheirolepidiaceae and Podocarpaceae might also have contributed to the resin production (Perrichot 2004, 2005).

DISCUSSION

Without having all amber pieces examined, nearly 900 biological inclusions are recorded so far from ten newly reported fossiliferous Cretaceous deposits, with about 760 inclusions from the Late Albian amber of Archingeay-Les Nouillers (Table 2). This fossil assemblage is mainly composed of insects but also contains other arthropods such as Arachnida, Crustacea and Myriapoda (Fig. 2A), vertebrate remains such as a reptile skin (Perrichot & Néraudeau 2005) and several feathers, plant remains (wood) and various micro-organisms (bacteria, fungi, algae, diatoms, dinoflagellates, etc.). Micro-inclusions are not considered here because studies of these organisms have only just started. For arthropods, numerous taxa are still not identified beyond the order or family level and require further analyses. However, significant new records and taxa already occur.

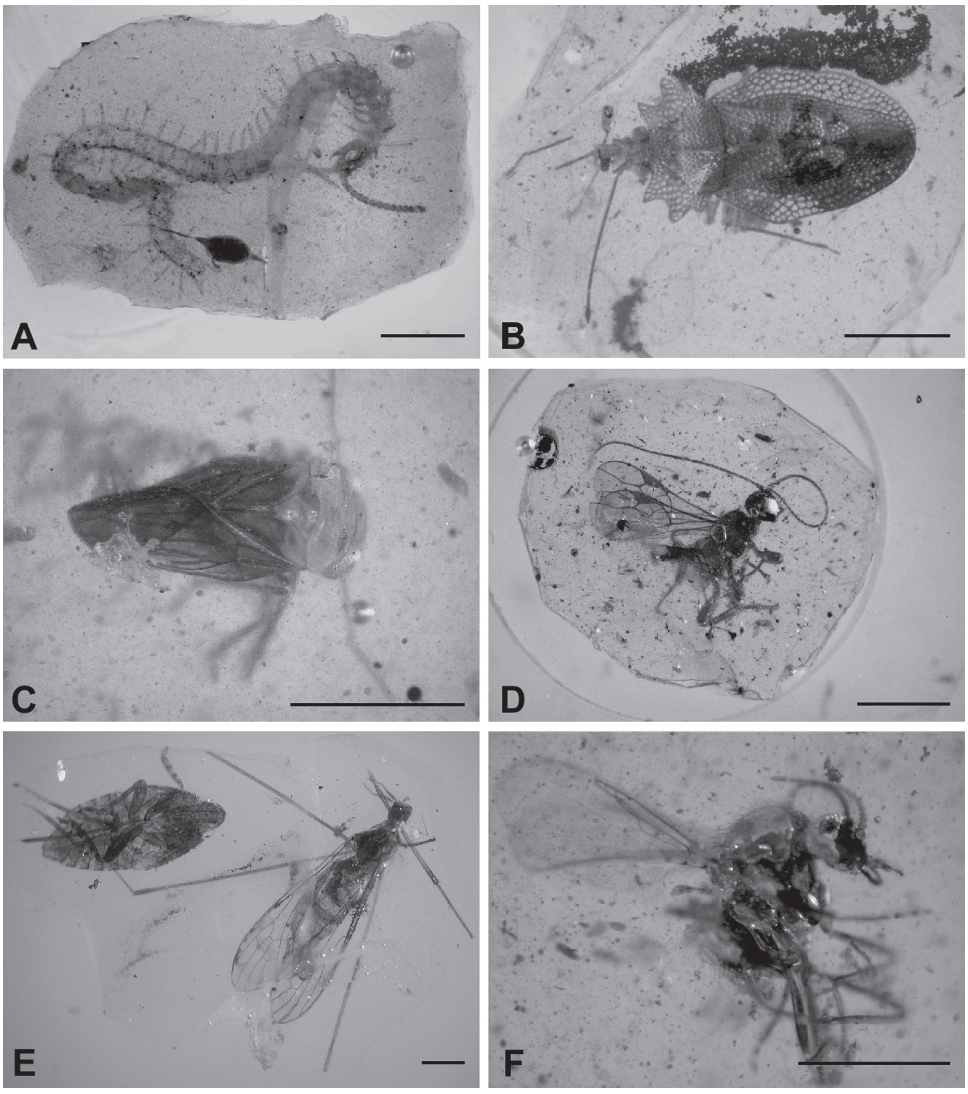

Fig. 2. Various arthropod inclusions in the Late Albian amber of SW France: (A) Chilopoda, MNHN Buz 1.8, La Buzinie; (B) Heteroptera Tingidae, MNHN Cdl 2.28, Cadeuil; (C) Heteroptera Schizopteridae, MNHN Buz 1.5, La Buzinie; (D) Hymenoptera Braconidae, Protorhyssalinae, MNHN Cdl 2.30, Cadeuil; (E) Diptera Limoniidae and Hemiptera Achilidae, MNHN Arc 186.2, Archingeay-Les Nouillers; (F) Diptera Ceratopogonidae, MNHN Cdl 2.1, Cadeuil. Scale bars = 1 mm.

Arachnida

Arachnids form about 9% of total arthropod inclusions in the Albian amber of France, while they are nearly absent from the Cenomanian amber. Two Pseudoscorpionida and a Scorpiones of the extinct family Palaeoeuscorpiidae (Lourenço 2003) are recorded, but most are Acari and Araneae.

TABLE 2

List of inclusions newly reported from the Cretaceous amber of France.

Group	Taxon	
ARCHINGEAY– Late Albian		
Kingdom Plantae		
Conifera (wood)	Araucariaceae [#]	many
Kingdom Animalia		
Phylum Vertebrata		
Reptilia (skin)	indet. [#]	1[a]
feathers	indet.	7
Phylum Arthropoda		
Isopoda	indet.	11
Tanaidacea	indet.	1
Diplopoda	Polyxenida indet.	1
Myriapoda	indet. [#]	1
Pseudoscorpionida	Cheliferidae	2
Scorpionida	Palaeoeuscorpiidae [#]	1[b]
Acari	indet.	39
Araneae	Zodariidae	3
	indet.	23
	TOTAL	26
Collembola	indet.	11
Strepsiptera	indet.	6
Blattodea	Umenocoleidae	1
	indet.	29
Dermaptera	indet.	5
Isoptera	indet. [#]	2
Orthoptera	Gryllotalpidae	2[c]
	Grylloidea	7
	Tridactylidae	6
	Acridoidea?	2
	indet.	14
	TOTAL	31
Sternorrhyncha	Coccoidea	7
Auchenorrhyncha	Achilidae	4
	Fulgoroidea	9
	TOTAL	13
Heteroptera	Gerridae	2[d]
	Gerromorpha indet.	1[d]
	Schizopteridae	2[e]
	Tingoidea	2[f]
	indet.	5
	TOTAL	12
Hemiptera	indet.	4
Psocoptera	Trogiomorpha	8[g]
	indet.	18
	TOTAL	26
Thysanoptera	Thripidae?	1
	indet.	1
	TOTAL	2
Raphidioptera	Mesoraphidiidae? [8]	1
Neuroptera	Ascalaphidae [8]	1
	Myrmeleontidae[8]	3
	Rhachiberothidae	1[h]
	Coniopterygidae	1[i]
	indet.	1
	TOTAL	7
Coleoptera	Buprestidae	1
	Curculionoidea	1
	Elateridae	1
	Ripiphoridae	2[j]
	Scraptiidae	1
	Staphylinioidea	2
	indet. [#]	25
	TOTAL	33
Lepidoptera	indet.	5
Hymenoptera	Ceraphronoidea	3[k,l]
	Chalcidoidea	31
	Cynipoidea	3
	Diapriidae	1[l]
	Formicidae	14[m]
	Ibaliidae?	1
	Ichneumonidae? [#]	2
	Proctotrupoidea	1
	Scelionidae	11[l]
	Siricidae?	1
	Sphecidae?	1
	Trigonalidae	1[n]
	indet.	28
	TOTAL	98
Diptera	Bombyliidae? [#]	1
	Cecidomyiidae	1
	Ceratopogonidae	35
	Chironomidae	8
	Dolichopodidae	45[o]
	Hilarimorphidae?	1
	Limoniidae	3[p]
	Mycetophiloidea	1
	Phoridae	2
	Psychodidae	18[q]
	Rhagionidae	4
	Tipuloidea indet. [#]	8
	Brachycera indet. [#]	105
	Nematocera indet. [#]	43
	indet. [#]	45
	TOTAL	320
Insecta	indet. [#]	65
	TOTAL, inclusions	760
CADEUIL – Late Albian		
Acari	indet.	3
Blattodea	indet.	2
Auchenorrhyncha	Fulgoroidea	1
Heteroptera	Tingidae	1
Psocoptera	indet.	1
Thysanoptera	indet.	1
Coleoptera	indet. [#]	1
Lepidoptera	indet.	1
Hymenoptera	Braconidae	2[l]
	Ceraphronoidea	2[l]

Group	Taxon	
CADEUIL (continued)		
Hymenoptera	Chalcidoidea	2
	Megalyridae	1[l]
	Scelionidae	4[l]
	Scolebythidae	1[l]
	indet.	5
	TOTAL	17
Diptera	Ceratopogonidae	4
	Chironomidae	2
	Dolichopodidae	3
	Psychodidae	1
	Nematocera indet. [#]	1
	Brachycera indet. [#]	5
	TOTAL	15
	TOTAL, inclusions	44
LES RENARDIÈRES – Late Albian		
Diptera	Nematocera indet. [#]	2
LA BUZINIE – Early Cenomanian		
Kingdom Plantae		
Conifera (leaf)	indet.	1
Kingdom Animalia		
Tanaidaceae	indet.	2
Chilopoda	indet.	1
Acari	indet.	1
Collembola	indet.	1
Blattodea	indet.	1
Heteroptera	Schizopteridae	2[e]
Diptera	Dolichopodidae	9
	TOTAL, inclusions	17
FOURAS – Early Cenomanian		
Araneae	indet. [#]	1
Acari	indet.	3
Coleoptera	Nitidulidae	1
Sternorrhyncha	Aleyrodidae	1
Hymenoptera	Formicidae	2[m]
	Scelionidae	5[l]
	indet.	1
	TOTAL	8
Diptera	Ceratopogonidae	4
	Dolichopodidae	1
	Phoridae?	1
	Brachycera indet. [#]	1
	Nematocera indet. [#]	2
	TOTAL	9
Insecta	indet.	2
	TOTAL, inclusions	25
AIX ISLAND – Early Cenomanian		
Trichoptera	indet.	1
Diptera	indet. [#]	1
Hymenoptera	Formicidae?	1
	TOTAL, inclusions	3

Group	Taxon	
FOURTOU – Early Cenomanian		
Tanaidacea	indet.	6
Hemiptera	indet.	1
Hymenoptera	Scelionidae	1[l]
	Stigmaphronidae	1
	indet.	3
	TOTAL	5
Diptera	indet.	17
	TOTAL, inclusions	29
SALIGNAC – Cenomanian		
Diplopoda	Synxenidae	1[r]
Heteroptera	Tingoidea	1[f]
Coleoptera	Ripiphoridae	1[j]
Diptera	indet.	12
	TOTAL, inclusions	15
PIOLENC – Santonian		
Hymenoptera	indet.	6
Diptera	indet.	9
	TOTAL, inclusions	15
BELCODENE – Santonian		
Diptera	indet.	1[#]
TOTAL, Cretaceous amber of France		911

[8] Larvae; [#] fragments; [a] Perrichot & Néraudeau 2005; [b] Lourenço 2003; [c] Perrichot *et al.* 2002; [d] Perrichot *et al.* 2005; [e] Perrichot *et al*. in press; [f] Perrichot *et al*. 2006; [g] Perrichot *et al.* 2003; [h] Nel *et al.* 2005*b*; [i] Nel *et al.* 2005*a*; [j] Perrichot *et al.* 2004*a*; [k] fam. incertae sedis, Perrichot *et al.* 2004*b*; [l] Perrichot *et al.* in prep.; [m] Perrichot *et al.* submitted; [n] Nel *et al.* 2003; [o] Nel *et al.* 2004*c*; [p] Perrichot *et al*. 2007; [q] Azar *et al.* 2003; [r] Nguyen Duy-Jacquemin & Azar 2004.

Within spiders, three specimens have been identified as members of the family Zodariidae. They show the unusual reduction of spinnerets characteristic of the family. The arrangement of eyes and the positioning of the legs give them a systematic position close to the subfamily Zodariinae. Interestingly, modern Zodariinae are specialised predators feeding exclusively on ants (Pekár & Křál 2002). Thus, the presence of zodariids together with that of several ants in the same deposit suggests that such a predator-prey relationship could have existed since the Early Cretaceous at least. Other fossil Zodariidae are extremely scarce, being mentioned in Eocene Baltic amber only (Wunderlich 1995).

So far, the Cretaceous family Lagonomegopidae is not reported from French amber. This is somewhat surprising, considering its presence in ambers from Siberia, New Jersey, Canada, Myanmar and Spain (Eskov & Wunderlich 1994; Penney 2002, 2004, 2005, 2006). Among the major fossiliferous Cretaceous amber deposits, Lagonomegopidae are absent only from Lebanon and France.

Heteroptera

Gerromorpha: Mesozoic gerromorphan or semi-aquatic bugs are rather scarce, although Andersen (1998) estimated a Jurassic divergence of most of the eight extant families. The only fossils known thus far are four Cretaceous records: two representatives of the family Hydrometridae from the Aptian Santana Formation of Brazil and from the Albian Burmese amber (Nel & Popov 2000; Andersen & Grimaldi 2001), and Veliidae and Mesoveliidae from the Aptian of the Koonwarra fossil beds in Australia (Jell & Duncan 1986). The oldest known fossil Gerridae, a sister family of the Veliidae, and one Gerromorpha of undetermined family are recorded in the Albian amber of Archingeay-Les Nouillers. A description and discussion is provided elsewhere (Perrichot *et al.* 2005*a*).

Cimicomorpha: Tingoidea are represented by the family Tingidae in the Albian amber of Cadeuil (Fig. 2B), and by a family *incertae sedis*, similar to Vianaididae, in the Albian and Cenomanian amber of Archingeay-Les Nouillers and Salignac. The Tingidae would be the only Mesozoic and the oldest known representative of the family as Nel, Waller and De Ploëg (2004) considered the two Lower Cretaceous genera *Golmonia* and *Sinaldocalder* (Popov 1989) as Heteroptera *incertae familiae*. So far, 38 fossil species of Tingidae have been described, all of Cainozoic age (Wappler 2003; Nel, Waller & De Ploëg 2004).

According to Schuh and Slater (1995), the Gerromorpha is the sister group of the Panheteroptera (=Nepomorpha + Leptopodomorpha + Pentatomorpha + Cimicomorpha). The finding of new representatives of both the Cimicomorpha and Gerromorpha in the Albian and Cenomanian French amber is thus of considerable significance for the phylogeny and chronology of the "higher" Heteroptera (=Panheteroptera).

Dipsocoromorpha: This is one of the most primitive groups within the true bugs (Heteroptera). Four specimens of the family Schizopteridae, or jumping ground bugs, are recorded from the Late Albian amber of Archingeay-Les Nouillers and the Early Cenomanian amber of La Buzinie at Champniers (Fig. 2C). They represent a new genus very similar to the extant *Hypselosoma*, suggesting great morphological stability of this small bug family whose fossil record is very sparse. Cainozoic specimens are recorded from the Oligocene–Miocene Dominican and Mexican ambers, and from the

Eocene Baltic amber. Mesozoic fossils are mentioned from the Albian Burmese and Neocomian Lebanese ambers (Poinar 1992; Popov & Herczek 1993; Grimaldi *et al.* 2002), but none of these fossils has been described thus far. The Schizopteridae and Tingoidea are described and discussed elsewhere (Perrichot *et al*. 2006, in press).

We hypothesise that the Dipsocoromorpha: Enicocephalidae could also occur in the French Cretaceous amber, as this is a sister group of the Schizopteridae (according to Schuh & Slater 1995) and because several representatives have been found in the Lebanese and Burmese ambers (Azar *et al.* 1999; Grimaldi *et al.* 2002).

Coleoptera

Compared with other Cretaceous ambers, Coleoptera are rather infrequent in both the Albian and Cenomanian deposits, comprising about 4% and 1% of the total arthropod inclusions respectively. The oldest Ripiphoridae are recorded as two distinct genera: the extinct *Paleoripiphorus* from the Albian amber of Archingeay-Les Nouillers and the extant genus *Macrosiagon* from the Cenomanian amber of Salignac (Perrichot *et al.* 2004*a*). Grimaldi *et al.* (2002) reported, but did not describe, the only other known Cretaceous specimen, from Burmese amber, and rare ripiphorids are reported from the Eocene Baltic amber and the Palaeogene of Florissant (Kaup *et al.* 2001; Meyer 2003). Other beetles assigned to Buprestidae, Elateridae, Nitidulidae, Scraptiidae, Staphylinidae and Curculionoidea also occur, but the specimens have yet to be studied.

Neuroptera + Raphidioptera (Neuropterida)

These are quite uncommon with only eight specimens from Archingeay-Les Nouillers, almost all being larvae. Six specimens belong to the neuropteran families Ascalaphidae, Myrmeleontidae, Rhachiberothidae (Nel *et al.* 2005*b*) and Coniopterygidae. Within the latter, the specimen is the oldest representative of the extant tribe Fontenelleini of the subfamily Aleuropteryginae (Nel *et al.* 2005*a*). One raphidiopteran specimen is represented by the head capsule of a larva. The distinct collar visible in all extant raphidiopteran larvae (Aspöck 1998) is absent here, as in the two other Cretaceous snakefly larvae previously described with two adult forms from the Burmese and New Jersey ambers (Grimaldi 2000; Engel 2002). Thus, the larval specimen probably belongs to the same extinct family Mesoraphidiidae. Among Cretaceous ambers, it is the fourth larva and the sixth specimen for this family, the only other specimen being an undescribed head of a larva from Lebanon. This specimen gives further evidence of the past distribution of snakeflies in tropical habitats, whereas today they are restricted to temperate regions of the Northern Hemisphere (Aspöck 1998).

Hymenoptera

Hymenoptera is the second largest group, after Diptera, in terms of the number of specimens (14% and 11% for the Albian and Cenomanian ambers respectively), but the largest in terms of diversity, with 12 families recognised and at least three others still undetermined. This hymenopteran fossil assemblage is somewhat distinct, both in present groupings and relative abundance, compared to other fossiliferous Cretaceous ambers.

Symphytans are exceptionally rare in amber: Orussidae have been described only from New Jersey (Basibuyuk *et al.* 2000) and Siberia (Rasnitsyn 1977). In Spain, another specimen of this family and one Anaxyelidae have been found, but are not yet described

(Martínez-Delclòs *et al*. 1999). The amber from Archingeay-Les Nouillers contains a putative Siricidae, but further preparation of the inclusion is needed for an accurate systematic attribution due to the very cloudy aspect of the amber piece.

All other Hymenoptera discovered in the French ambers are apocritans, and Parasitica make up 85% of the total hymenopteran specimens belonging to at least 12 families: Trigonalidae, Megalyridae, Stigmaphronidae, Scelionidae, Diapriidae, Ibaliidae, Braconidae, Ichneumonidae and yet undetermined families of the Ceraphronoidea, Proctotrupoidea, Chalcidoidea and Cynipoidea. Aculeata belong to the families Scolebythidae, Sphecidae and Formicidae. Chalcidoidea dominate in this assemblage but are not yet studied at the family level. Scelionidae is the most abundant family with 24% of all specimens collected, represented by four distinct genera and five species. It is not surprising that they are common and diverse, as in all Cretaceous ambers, as this group appeared during the Early Cretaceous and diversified extensively during the mid-Cretaceous (Rasnitsyn 2002). More surprisingly, Formicidae is the second largest family, representing 12% of all hymenopteran specimens.

The Trigonalidae is the oldest described fossil representative of this family (Nel *et al.* 2003), but several specimens are recorded in the Aptian amber of Álava, Spain (Martínez-Delclòs *et al.* 1999). Within Diapriidae, the oldest representative of Belytinae is recorded, with previous accurate records not being mentioned before the Eocene. Two specimens found in the Albian amber of Cadeuil belong to the Protorhyssalinae (Fig. 2D) and are the second and oldest occurrence of this extinct braconid subfamily, which was previously described only from the Turonian amber of New Jersey (Basibuyuk *et al.* 1999). Lastly, five ants are recorded in at least three distinct genera: a putative worker of uncertain subfamily in the extinct genus *Gerontoformica* (Nel *et al.* 2004*b*), an alate female and an incomplete worker closely resembling the extinct Burmese amber genus *Haidomyrmex* Dlussky, 1996, and two sphecomyrmine workers of the extinct Burmese amber genus *Sphecomyrmodes* Engel & Grimaldi, 2005 (Perrichot *et al.* submitted-*b*). In addition, 11 inclusions are putatively attributed to the Formicidae, but they are preserved in opaque amber and need further analysis for accurate identification. So far, they are the oldest known ants together with those from the contemporaneous Burmese amber. Descriptions and further discussions of all these apocritans, with the exception of Ibaliidae, Sphecidae, Stigmaphronidae, Proctotrupoidea, Chalcidoidea and Cynipoidea, are provided elsewhere (Nel *et al.* 2003, 2004*b*; Perrichot *et al.* 2004*b*, in prep.).

Diptera

Diptera is the most abundant group of inclusions in both the Albian and Cenomanian ambers of France (43% and 23% respectively), as in all fossiliferous resins. Similarly, Dolichopodidae, Ceratopogonidae, Psychodidae and Chironomidae dominate (nearly 37% and 74% of all dipteran inclusions for Albian and Cenomanian respectively). Detailed analysis is needed in order to evaluate the diversity in each family.

Within dolichopodids, a new species of the microphorine genus *Microphorites* is common and largely dominant (Nel *et al.* 2004*c*), but at least two other undetermined genera also occur. *Microphorites* was previously described from the Lebanese amber (Hennig 1971; Grimaldi & Cumming 1999) and mentioned in Burmese and Spanish ambers (Grimaldi *et al.* 2002). The psychodids are almost exclusively represented by a

new species of *Eophlebotomus*, an extinct genus occurring in the Lebanese and Burmese ambers (Cockerell 1920; Duckhouse 2000; Azar *et al.* 2003). In addition, two distinct genera have been found in the Albian amber of Archingeay-Les Nouillers and Cadeuil, belonging to the subfamily Sicoracinae or Trichomyinae. Finally, Tipuloidea are rather common inclusions in amber from Archingeay-Les Nouillers. Almost all are incomplete and represented by wings or legs only, but three Limoniidae of the genus-group *Limonia* are preserved (Fig. 2E; Perrichot *et al.* 2007). This is the oldest record of the genus *sensu lato*, which is frequently found fossilised in the Tertiary of Europe (Evenhuis 1994) but rather infrequently in the Cretaceous, being described only from the Turonian amber of New Jersey (Gelhaus & Johnson 1996) and the Campanian amber of Canada (Krzemiński & Teskey 1987).

Ceratopogonidae or biting midges are common and abundant (Fig. 2F) as in all Cretaceous ambers. Szadziewski and Schlüter (1992) described three genera in the Cenomanian amber of NW France: *Atriculicoides*, *Leptoconops* and *Austroconops*. Thus, we predict that these genera may occur in the Albian and Cenomanian amber presented herein. Other genera such as *Minyohelea*, *Protoculicoides* and *Archiaustroconops* could also be expected, due to their occurrence in ambers from Lebanon, Myanmar or Spain (Szadziewski 1996, 2004; Szadziewski & Arillo 1998; Borkent 2000) where dipteran assemblages show common taxa (e.g., *Microphorites*, *Eophlebotomus*).

CONCLUSION

With 26 arthropod orders and numerous other biological inclusions recorded in eight Albian and Cenomanian amber deposits, the present analysis of newly recovered material demonstrates that the palaeontological significance of the mid-Cretaceous amber of France was hitherto underestimated. Actually, this amber, together with ambers from Lebanon, Spain, Myanmar, New Jersey, Canada and Siberia, rates as one of the seven major fossiliferous Cretaceous ambers.

During the mid-Cretaceous, the Charente-Maritime region was composed of a mosaic of coastal habitats with peculiar plant associations, from littoral to lacustrine environments and intermediate mangrove-like areas, under a warm and wet subtropical climate but with probable arid seasons (Moreau 1993; Néraudeau *et al.* 2002, 2003, 2005; Perrichot 2004, 2005; Gomez *et al.* 2004; Videt 2004; Dejax & Masure 2005). The amber-producing forest, mainly composed of Araucariaceae, Podocarpaceae and Cheirolepidiaceae (Perrichot 2005), was probably located in this mangrove-like environment. Indeed, there is evidence that the resin could have flowed directly into brackish water: diatoms, dinoflagellates and cyanobacteria characteristic of this type of environment have been found as micro-inclusions in many amber pieces (Breton & Tostain 2005), and typically marine arthropods are also included within the fossilised assemblage (e.g., Crustacea Tanaidacea and Heteroptera Gerridae). The rest of the arthropod assemblage is consistent with such an environment, with numerous representatives of the ground habitat of humid forests preserved in the "litter amber" (Perrichot 2004). The important number and variety of predators and parasites suggest a high diversity for the biocenosis of the original ecosystem.

Schlüter (1978) and Breton and Tostain (2005) proposed a similar palaeoenvironmental reconstruction for the Cenomanian deposits of NW France. Despite these similarities, some differences occur in the taxonomic diversity observed between amber from the

two regions: some groups described by Schlüter (1978) in the amber of NW France are absent from the amber of SW France (e.g., Hymenoptera: Mymaridae and Falsiformicidae, Diptera: Keroplatidae), and when a family is found in both ambers, subordinate taxa are different (e.g., Neuroptera: Rhachiberothidae, Hymenoptera: Diapriidae). So far, only the Cenomanian amber of Fourtou (Corbières) has yielded a scelionid wasp similar to that of the amber from Bezonnais, NW France (e.g., *Cenomanoscelio pulcher*). Full appreciation of the diversity of the French Cretaceous ambers will require further detailed studies.

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A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples

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ABSTRACT

A comprehensive comparison is provided for the first time for arthropod-assemblage compositions in Rovno and Baltic ambers, based on representative samples from Klesov (Pugach) and Dubrovitsa (Vol'noje) quarries (1256 fossils) and Yantarny quarry (757 fossils), respectively. A representative collection of Baltic amber was taken in Yantarny at the local mining factory (only smaller pieces that fitted through a 32 mm sieve were selected). A representative collection of Rovno amber was taken at the factory "UkrAmber" (Rovno). Results indicate the compositions of the assemblages to be different enough to consider the origin of Rovno and Baltic ambers as geographically different. The relative abundance of mites (Acari) in the Rovno sample is 0.6 times that in the Baltic sample (the share of dominant "*Acarus*" *rhombeus* Koch & Berendt in the Rovno smple is 0.3 times that in Baltic amber), and the relative abundance of Homoptera in the Rovno sample is almost half of that in the Baltic sample (mainly due to relative rarity of both the dominant aphid *Germaraphis*, whose share is 0.2 times that in the Baltic sample, and the scale insects). Within Diptera, the proportion of Chironomidae is almost half, and Sciaridae twice that of the Baltic sample. In terms of ants (Formicidae), the proportion of *Ctenobethylus goepperti* (Mayr) in the Rovno sample is half of that in the Baltic sample. The most striking are differences in species-level composition: 9 of 37 ants found in the Rovno representative sample belong to species and genera unknown in Baltic amber. Some differences encountered are of an ecological nature: aquatic and subaquatic arthropods are comparatively rare and leaf-litter dwellers of the *Sciara* zone are very abundant in Rovno amber. The age of the Baltic amber and stratigraphic correlation of the amber-bearing Prussian Formation are also considered in some detail. It is concluded that the proposal for their Ypresian–Lutetian age contradicts a wide array of the palaeontological, radiological, and stratigraphic data and thus cannot be accepted on the basis of available evidence.

KEY WORDS: Amber, Baltic, Rovno, Arthropoda, Insecta, faunal assemblage, inclusions, Eocene.

INTRODUCTION

The Late Eocene Baltic amber fauna has already been examined for more than 200 years. During this period, over 3000 species of animals and more than 100 species of plants have been described or indicated (Zherikhin 1978; Rasnitsyn & Quicke 2002). No other fossil locality is comparable with Baltic amber in terms of this diversity, and amber inclusions undoubtedly belong to those most widely known among lay people. Such a reputation does not, however, guarantee irrefutable knowledge of the Baltic amber fauna (Zherikhin & Eskov, in press). One of the problems yet to be resolved is the primary composition of the amber fauna. The available collections are biased because of overrepresentation of the most spectacular, rare, or otherwise more interesting inclusions, and this is at the expense of other 'trivial' fossils. This problem may be solved only by purposeful creation and study of representative collections whose original taxonomic composition of the fossil assemblage is minimally modified.

Previously, the only sample of the Baltic amber considered representative (that is, with minimally distorted original taxonomic composition of the fossil assemblage) was

the collection from Palmnicken (now Yantarny) described by Klebs (1910), further referred to as Klebs Coll. Recently, another representative collection which is kept at the Museum of Amber Inclusions at The University of Gdańsk has been described (Sontag 2003), further referred to as Sontag Coll. Unfortunately, its origin has been insufficiently specified ("3875 pieces of Baltic amber from Samland deposits (42.6 kg)" (Sontag 2003: 432).

The comparison of Klebs Coll. with Sontag Coll. and those described below indicates that the status of Klebs Coll., as a representative one, is not beyond doubt. Within Klebs Coll., the main problem is not even a low number of Acari (pointed out by Sontag who believes that this under-representation is a result of low-quality instruments used by Klebs). More serious is an unrealistically high abundance of Trichoptera compared to very low numbers of Hymenoptera (5.6% and 5.1% of all inclusions, respectively). The main problem is, however, different: Klebs used either the same source of amber as Sontag did, or one near-by. Being aware of the most productive varieties of the amber, Klebs nevertheless selected only 12 400 animal inclusions from 200 kg of amber with layered structure, while Sontag Coll. includes 42.6 kg of "unselected amber with layered structure" (Sontag 2003: 432), of which 1824 pieces weighing 22.3 kg, contained 7111 animal inclusions. In their material, the average weight of a piece of raw amber is similar (8.9 g in Klebs Coll. vs. 11 g in Sontag Coll.). At the same time, in Sontag Coll., an average inclusion-bearing piece of amber contains nearly three times more inclusions (3.9, or 0.32 inclusion per g) than in Klebs Coll. (1.6, or 0.17 per g). Given these discrepancies, it is not reasonable to consider Klebs Coll. as one that is truly representative.

Hoffeins and Hoffeins (2004) initiated a comparative study of the fauna of the Baltic and Bitterfeld (Saxonian) amber, driven by the inconsistency between Klebs's trichopteran data and their own results. They present statistics of inclusions in two big representative collections of the Baltic and Bitterfeld amber. The former collection originates from 11 different geographical sources taken together (further referred to as Hoffeins Baltic Coll.). The results found are unexpectedly similar for both collections, thus closing the discussion regarding the independent origin of Bitterfeld amber. The results obtained by Hoffeins and Hoffeins (2004) are in agreement with ours. This allows us an opportunity to use their data as representative collections of Baltic and Bitterfeld amber, within our analysis.

It should be mentioned that the proportion of Acari found in their collections is lower than in ours: the volume of gathered and examined collections is tremendous (574.3 kg), and thus it is possible that parts of small mites may have gone unnoticed. Our experience suggests that a more or less thorough selection of mites is possible only after multiple (more than ten times) examinations of one and the same sample. This, however, becomes an impossible task when faced with more than half a ton of amber.

Questions regarding the relationship between Baltic and Rovno amber, in addition to their areas of origin, have remained unresolved until recently. The reason for this is that there has been an absence of data on the fauna from Rovno amber.

To fill this gap, researchers from the Paleontological Institute, Russian Academy of Sciences (Moscow), and the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (Kiev), undertook special efforts to raise representative collections

TABLE 1

Representation of the main taxonomic groups of arthropods in the representative samples of Baltic (Brighton Coll., Sontag Coll., Hoffeins Baltic Coll.), Bitterfeld (Hoffeins & Hoffeins, 2004) and Rovno amber.*

Taxa	Brighton Coll.	Sontag Coll.	Hoffeins Baltic Coll.	Hoffeins Bittefeld Coll.	Representative Rovno Coll.
Pseudoscorpiones	2	+	6 (0.1%)	21 (0.1%)	1
Opiliones	3 (0.4%)	+	10 (0.1%)	25 (0.2%)	4 (0.3%)
Aranei	24 (3.2%)	4.9%	359 (5.0%)	909 (6.1%)	40 (3.2%)
Acari	204 (27.0%)	24.0%	998 (13.9%)	2492 (16.8)	198 (16.0%)
Myriapoda	3 (0.4%)	+	17 (0.2%)	29 (0.2%)	2
Collembola	42 (5.6%)	8.0%	686 (9.6%)	1213 (8.2%)	86 (7.0%)
Archaeognatha	1	+	15 (0.2%)	16 (0.1%)	5 (0.4%)
Ephemeroptera	–	+	3	9	3
Odonata	–	–	1	1	–
Psocoptera	4 (0.5%)	+	37 (0.5%)	62 (0.4%)	5 (0.5%)
Thysanoptera	3 (0.4%)	0.7%	33 (0.5%)	44 (0.3%)	6 (0.5%)
Aphidoidea	31 (4.1%)	2.6%	321 (4.5%)	673 (4.5%)	24 (2.0%)
other Hemiptera	10 (1.3%)	1.9%			23 (1.9%)
Strepsiptera	–	–	2	–	–
Coleoptera	15 (2.0%)	3.0 %	312 (4.4%)	693 (4.7%)	64 (5.2%)
Neuroptera *s.l.*	–	+	4	6	–
Mecoptera	1	–	–	1	–
Trichoptera	2	0.8%	48 (0.7%)	81 (0.5%)	9 (0.7%)
Lepidoptera	7 (1.0%)	+	23 (0.3%)	70 (0.5%)	7 (0.6%)
Diptera	342 (45.3%)	42.7%	3676 (51.2%)	7128 (48.1%)	626 (50.7%)
Nematocera	279 (37.0%)	33.3%	2929 (40.8%)	5685 (38.4%)	518 (41.9%)
Brachycera	58 (7.7%)	5.8%	738 (10.3%)	1426 (9.6%)	104 (8.4%)
Formicidae	22 (2.9%)	3.7%	556 (7.7%)	1205 (8.1%)	37 (3.0%)
other Hymenoptera	28 (3.7%)	2.9%			50 (4.1%)
Blattoptera	2	+	31 (0.4%)	55 (0.4%)	5 (0.4%)
Isoptera	1	+	16 (0.2%)	33 (0.2%)	3
Mantodea	–	–	1	–	–
Plecoptera	–	+	4	2	–
Embioptera	1	–	–	–	1
Dermaptera	–	–	1	1	–
Orthoptera	1	–	8 (0.1%)	11 (0.1%)	–
TOTAL	755	6906	7177	14 808	1236

* Figures in the Total row differ from those given in various places in the text for the following reasons: 755 (not 757) in the Brighton Coll. column and 1236 (not 1256) in the Representative Rovno Coll. column differ because within the Arachnids, records which are based on the identification of particular spider webs, and not the actual specimens themselves, are not included; 7177 (not 7168) in the Hoffeins Baltic Coll. column, and 14 808 (not 14 780) in the Hoffeins Bitterfeld Coll. column differ because *incertae sedis* specimens are considered (although not shown separately in the table); the same for the Brighton Coll. (755, not 749) and the Representative Rovno Coll. (1236, not 1199).

of both Baltic and Rovno amber inclusions. A representative collection of Baltic amber has been extracted in Yantarny at the local mining factory (only pieces smaller than 32 mm were selected). Another representative collection, as well as the majority of other amber inclusions from the collection of the Schmalhausen Institute of Zoology, has been extracted in Rovno at the State Enterprise "UkrAmber" (only pieces of 2–50 g were selected). The present article is based on these two collections and includes published information concerning other representative collections. The purpose is to shed light on relationships between the respective entomofaunas.

TABLE 2

Composition of the arthropod fossils in Baltic amber (Brighton Coll.) and Rovno amber (Representative Rovno Coll.). Names of orders and higher level taxa are in bold; suborders are bold italic; genus and species names are italic and subfamilies of ants are given in brackets. Fossils not identified with confidence are considered in totals even if not shown in the table. The percentage of a particular order reflects the proportion of that order among all arthropods, and figures in brackets refer to the proportion of an insect order among Insecta *s.str.* Percentages of families and genera refer to proportions of those particular taxa within the corresponding order. Percentages may not be given for taxa represented by only one or two specimens in a particular sample. Figures are approximate.

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Pseudoscorpiones	**2**	**0.3**	**1**	
Dithidae: *Heterolophus* sp.	1		–	
Opiliones	**3**	**0.4**	**4**	**0.3**
Aranei	**24**	**3.2**	**40**	**3.2**
Amaurobiidae	1		–	
Araneidae	1		2	
Dysderoidea	1		–	
Nesticidae: *Acrometa cristata* Petrunkevitch	–		1	
Eusparassidae	1		–	
Oonopidae	2	8.3	5	12.8
Salticidae	2		2	
Linyphiidae	–		1	
Liocranidae	–		1	
Zodariidae: *Adorator* ?*hispidus* (Koch et Berendt)	–		1	
Theridiidae	5	21	13	33.3
Spider web	**2**	**0.3**	**20**	**1.6**
Acari	**204**	**27.0**	**198**	**15.8**
Digamasellidae	–		2	
Phytoseiidae	1		–	
?Ixodidae	–		2	
Gamasina indet.	–		1	
Parasitiformes indet.	1		–	
Glycyphagidae: "*Acarus*" *rhombeus* Koch et Berendt	116	56.9 (15.3 of all arthropods)	62	31.3 (4.9 of all arthropods)
Astigmata (Acaridia) indet.	–		7	3.5
Oribatei: cf. *Licneremaeus fritschi* Sellnick	1		–	
Damaeidae	1		–	
Oppoidea	–		1	
?Cepheidae	–		1	
Liacaroidea	–		1	
Brachypilina indet.	–		1	
Oribatida indet.	18	8.8	14	7.0
Bdellidae	–		1	
?Rhagidiidae	–		1	
Anystidae	–		9	4.6
Cheyletoidea	–		2	
Erythraeidae	–		4	2.0
Microtrombidiidae	–		5	2.5
Parasitengona indet.	–		9	4.6
Trombidiiformes indet.	54	26.5	4	2.0
Acari indet.	12		71	
Diplopoda	**3**	**0.4**	**1**	
Polyxenidae: *Polyxenus* sp.	2		1	
Chilopoda: Lithobiidae: *Lithobius* sp.	–		**1**	
Collembola	**42**	**5.6**	**86**	**6.9**
Entomobryidae	16	38.1	46	54
Tomoceridae	–		1	
Entomobryomorpha indet.	6		5	
Hypogastruridae	–		3	3.5

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Sminthuridae	9	21.4	13	15.1
Bourletiellidae	–		2	
Symphypleona indet.	–		2	
Archaeognatha	**1**		**5**	**0.3 (0.4)**
Machilidae: *Machilis* sp.	–		5	
Ephemeroptera	–		**3**	
Psocoptera	**4**	**0.5 (0.8)**	**5**	**0.4 (0.6)**
Caeciliusidae	1		1	
Psocidae	2		1	
Sphaeropsocidae: *Sphaeropsocus kuenowii* Hagen	1		–	
Thysanoptera	**3**	**0.4 (0.6)**	**6**	**0.5 (0. 6)**
Homoptera	**41**	**5.4 (8.6)**	**43**	**3.4 (4.8)**
Sternorrhyncha	***39***	***5.2 (8.2)***	***32***	***2.6 (3.5)***
Elektraphididae: *Schizoneurites* sp.	2		–	
Mindaridae: *Mindarus* sp.	1		1	
Eriosomatidae: *Germaraphis* sp.	27	65.9 (5.7 of all insects)	10	23.4 (1.1 of all insects)
Drepanosiphidae	–		10	23.4
Aphidomorpha indet.	1		3	
Matsucoccidae: *Matsucoccus* sp.	2		2	
Ortheziidae	–		1	
Coccomorpha indet.	6		3	
Aleyrodidae	–		2	
Auchenorrhyncha	***2***		***11***	***0.9 (1.2)***
Cicadellidae	2		3	7.1
Heteroptera	–		**4**	**0.3 (0.4)**
Microphysidae: *Loricula perkovskyi* Putshkov & Popov	–		1	
Miridae	–		1	
Anthocoridae	–		1	
Coleoptera	**15**	**2.0 (3.2)**	**64**	**5.1 (7.1)**
Carabidae: *Dromius* sp.	1		–	
Staphylinidae	2	13.3	9	13.9
Pselaphinae	1		7	
Scydmaenidae	2	13.3	5	7.7
Ptiliidae	–		3	4.9
Melyridae	1	6.7	1	1.6
Helodidae	–		4	6.2
Anobiidae	3	20.0	1	1.6
Dryophilinae	2		–	
Cleridae	–		1	
Elateridae	–		7	10.8
Artematopidae	–		1	
Lathridiidae	1		1	
Zopheridae	–		1	
Languriidae	–		1	
Melandryidae	–		2	
Scraptiidae	1	6.7	2	3.1
Aderidae	1	6.7	5	7.6
Anthicidae	–		1	
Mordellidae	1	6.7	4	6.1
Curculionidae: Scolytinae	–		4	6.1
Polyphaga indet.	1		6	
Mecoptera				
Bittacidae: *Hylobittacus fossilis* (Carpenter)	**1**		–	
Trichoptera	**2**		**9**	**0.7 (1.0)**
Ecnomidae: *Archaeotinodes*? sp.	1		–	
Philopotamidae	–		1	
Polycentropodidae	–		3	33
Hydroptilidae	–		1	
Phryganeidae?	–		1	

TABLE 2 (*continued*)

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Lepidoptera	**7**	**0.9 (1.5)**	**7**	**0.6 (0.8)**
Gelechioidea	–		1	
Diptera	**342**	**45 (71.7)**	**626**	**50.0 (69.2)**
Nematocera	***279***	***37 (59)***	***518***	***41 (58)***
Tipulidae	–		4	0.6
Limoniidae	3	0.9	38	6.1
Tipuloidea indet.	2		9	
Ptychopteridae?	1		–	
Psychodidae	6	1.8	16	2.6
Chironomidae	139	40.6	137	21.9
Ceratopogonidae	20	5.9	29	4.6
Chironomoidea indet.	3	1.2	1	
Simuliidae	1		–	
Mycetophilidae	13	3.8	18	2.9
Keroplatidae	9	2.6	27	4.3
Mycetophilidae or Keroplatidae	2		10	
Mycetobiidae	–		1	
Sciaridae	52	15.2	189	30.1
Cecidomyiidae	24	7.0	23	3.7
Scatopsidae	–		3	0.5
Nematocera indet.	5		13	
Brachycera	***58***	***7.7 (12)***	***104***	***8.3 (12)***
Empididae	12	3.5	7	1.1
Dolichopodidae	38	11.1	64	10.2
Empidoidea indet.	1		–	
Bombyliidae?	–		1	
Rhagionidae	–		4	0.6
Syrphidae: Syrphinae	2		–	
Phoridae	3	0.9	18	2.9
Anthomyiidae?	1		–	
Diptera Schizophora indet.	1		–	
Brachycera indet.	–		10	
Hymenoptera	**50**	**6.6 (10.5)**	**87**	**6.9 (9.6)**
Megaspilidae	4	8	2	2.3
Ceraphronidae	–		1	
Bethylidae	–		1	
Proctotrupidae	1		–	
Diapriidae	6	12	8	9.2
Platygastridae	1	2	3	3.5
Scelionidae	3	6	16	18.4
Mymarommatidae	1	2	3	3.5
Mymaridae	3	6	5	5.8
Torymidae: *Monodontomerus* sp.	2		–	
Trichogrammatidae	–		2	
Aphelinidae	–		1	
Chalcidoidea indet.	1		–	
Ichneumonidae	3	6	–	
Braconidae	1	2	4	4.6
Ichneumonoidea indet.	1		–	
Formicidae	22	44 (4.6 of all insects)	37	43 (4.1 of all insects)
Blattoptera	**2**	**0.3 (0.4)**	**5**	**0.4 (0.5)**
Isoptera: Rhinotermitidae: *Reticulotermes antiquus* Heer	**1**		**3**	**0.2 (0.3)**
Embioptera	**1**		**1**	
Orthoptera Ensifera indet.	**1**		–	
TOTAL	757		1256	

MATERIAL

Baltic amber

Deposits bearing Baltic amber are abundant along the shores of the Baltic Sea from Lithuania to Jutland. In many places the amber was re-deposited, sometimes several times, as a result of erosion and glacial re-working of the amberiferous deposits.

The largest deposits are situated in Yantarny, Kaliningrad Region, and have been industrially mined since the end of the 19th century. The age of the richest amber-bearing deposits (so-called Blue Earth, or "Blau Erde" of German authors) is dated microfaunistically as Late Eocene (Kaplan *et al.* 1977).

These results have been questioned by Ritzkowski (1997), who inferred a Middle Eocene age of the Prussian Formation based on radiometrically dated glauconite from the lower layer of the Blue Earth (44.1±1 Ma) and the underlying Wild Earth (47.0±1.5 Ma). However, these figures are based on two samples, each from the respective layers. We consider these data to be insufficient to disprove the results by Kaplan *et al.* (1977) for the absolute glauconite age of the Prussian Formation (37.7±3 Ma), which was based on six samples. Furthermore, Grigelis *et al.* (1971) considers the glauconite of the Blue Earth and overlaying members of the Prussian Formation to be re-deposited. Further information is required to draw a final conclusion.

Further evidence stems from the presence of the zonal species *Globigerina corpulenta* (Subb.) in addition to a recent find of three species of planktonic foraminifers, viz. *Turborotalia centralis* (Cushm. & Bermudez), *Truncorotaloides* cf. *rohri* Bronn. & Bermudez, *Globigerina praebulloides* Blow., in the Prussian Formation of "Primorsky" quarry in Yantarny (Kharin & Lukashina 2002). These foraminifers are common in the Upper Eocene of the Lublin Province in Poland. These findings imply correlation of the Prussian Formation with the foraminiferal zones P15–P17 of the Upper Eocene (Kharin & Lukashina 2002). The presence of a dinoflagellate *Charlesdowniea clathrata* (Eis.) Lentin & Vozzhen. does not contradict the above data, because in the dinoflagellate zonation the respective zone is referred to the Priabonian Stage of the Upper Eocene (Krasheninnikov & Akhmetiev 1996: 26).

A rich foraminiferan assemblage of the Prussian Formation from Rudamina borehole (Lithuania) is characteristic strictly of the Upper Eocene (Grigelis *et al.* 1971). The sponge spicules of the Prussian Formation resemble those in the Upper Eocene of Dnieper-Donets Palaeogene Basin (Ivanik 2003: 66). Well-studied palynological assemblages of the Prussian Formation "are typical of the Upper Eocene of Western Europe, European part and other areas of CIS" (Krasheninnikov & Akhmetiev 1996: 26).

The Prussian Formation transgressively overlaps the Alkas Formation and lower Palaeogene formations and in the west of the Sambian Peninsula, it is overlaid by the Lower Oligocene Palve Formation. The assemblage of planktonic foraminifers of the Alkas Formation suggests its Bartonian age (Middle Eocene) (Kaplan *et al.* 1977). The glauconite absolute date of the Alkas Formation is 41±3.5 Ma (Bartonian/Lutetian boundary), and that of the Palve Formation is 34.6±3 Ma (Kaplan *et al.* 1977) (near the Eocene/Oligocene boundary according to Berggren *et al.* 1995). Taking into account the overlapping ranges of the foraminiferal P12–P14 and nannoplankton NP15–NP16 zones, Grigelis *et al.* (1988: 46) came to a conclusion regarding the identical stratigraphical position of the Baltic Alkas Formation and West Belorussian Kiev Formation

which "belong to the upper half of the Lutetian and to the Bartonian stages, and correspond to the Bodrakian Regio-Stage of Crimea". Thus, Ritzkowski's proposal (1997) of the Ypresian–Lutetian age of the Prussian Formation (Lower–lower Middle Eocene), and, consequently, the Bartonian age of the Palve Formation (upper Middle Eocene), if accepted, would result in reconsideration of the entire stratigraphy of the Middle Eocene–Lower Oligocene of Eastern Europe.

Ritzkowski (1997: 22) points out that the disparity in dates of amber-bearing deposits (those at Chłapowo in Pomorze, former Pomerania, correspond to the Eocene/Oligocene boundary) suggests that the Baltic amber fauna existed, without any essential changes, for more than 20 Ma ("all Eocene and the beginning of Oligocene"). This seems unlikely since, firstly, it is well known that none of the amber-bearing deposits can be considered as their primary burial, and this includes Chłapowo. Secondly and more importantly, the Middle and Late Eocene was a time of rapid change in the insect fauna, as reflected by a series of Lagerstätten ranging from the Middle Eocene Lutetian (Green River in the USA, Messel, Eckfeld and Geiseltal in Germany) through to near the Eocene/Oligocene boundary (Florissant in the USA, Bolshaya Svetlovodnaya in Primorskiy Krai and Bembridge Marls in England). The Baltic assemblage occupies an intermediate position between these two groups of faunas (Rasnitsyn & Quicke 2002; Dlussky & Rasnitsyn 2003). Thus, the hypothesis regarding long stasis of the entomofauna during the second half of the Eocene appears implausible. We plan to devote a special paper to the age of Baltic amber in the near future.

In the Yantarny quarries the amber is mined by washing away the "Blue Earth". The amber-bearing slurry is then piped into the industrial complex and successively sieved. In September 1992 and in June 1993 the team from the Arthropoda Laboratory, Paleontological Institute, Moscow, selected amber directly at the factory in Yantarny. A sample of raw amber was examined under the microscope, and the taxonomic position of all inclusions found was determined whenever possible, up to the order and family level. This level of identification is usually adequate in assessing the general composition of the fossil fauna. During two visits, 1382 (625+757) inclusions were found and identified. The collection of 1992 is included in a separate publication dealing mainly with the distribution of inclusions according to size fractions of the amber (Zherikhin & Eskov, in press). The composition of inclusions in the collection of 1993, as displayed at the order level in Table 1, and in more detail in Tables 2 & 3, is considered in this paper.

Rovno amber

Rovno amber with arthropod inclusions has been collected at the Klesov (the majority of inclusions), Dubrovitsa (less than one third of inclusions) and Vladimirets deposits (insignificant quantity) (all in the Rovno Region), which constitute a part of a vast area of the development of the amber-bearing layers in the north of the Rovno and Zhitomir regions, within the boundaries of Ukrainian Polesye (Perkovsky *et al.* 2003*a*). The industrial mining of amber in the Rovno Region began only recently. Before that, amber was taken in a primitive way from sandy-clay sediments of granite quarries in the outskirts of Klesov, from drainage-channel lumps, and from natural outcrops of amber-bearing deposits along river banks.

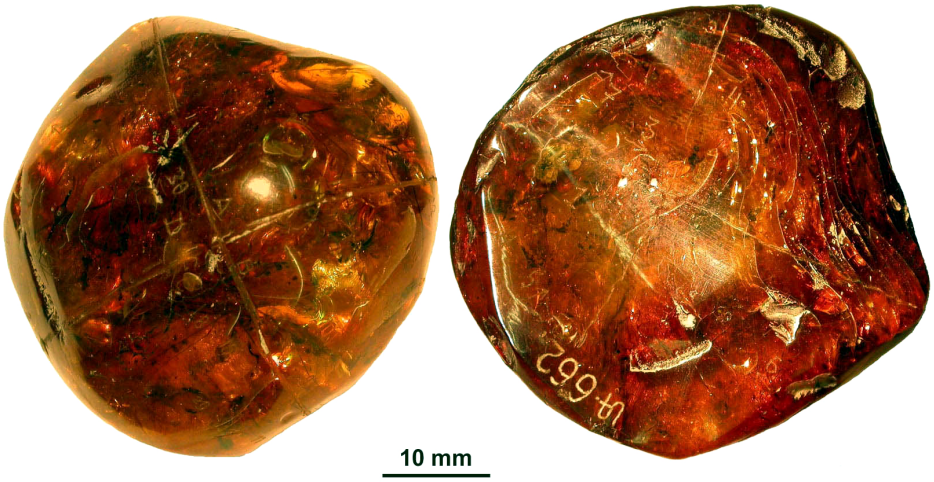

Fig. 1. A piece of Rovno amber (UA-662) with more than 50 inclusions.

The area where amber-bearing deposits developed is situated at the periphery of the north-western part of the Ukrainian Crystalline Rock Massif. Detailed information regarding the nature of Rovno amber deposits has already been published (Perkovsky *et al.* 2003*a*).

The Late Eocene age of the Obukhov Formation and the Early Oligocene age of the Mezhigorje Formation have been determined palaeontologically. According to A.B. Stotland (pers. comm.), dinocysts of the Obukhov Formation include index species of Zone *Charlesdowniea clathrata angulosa–Deflandria phosphoritica* and represent the zonal complex characteristic of the Obukhovian Regio-Stage in the stratotypical section, the Almian Regio-Stage of the Black Sea depression and Crimea, the Beloglinian Regio-Stage of the North Caucasus and the Priabonian Stage of Western Europe. The complex of palynomorphs with *Myrica pseudogranulata–Quercus gracilis–Q. gracili-formis* is also characteristic of Upper Eocene deposits of various regions in the south of the East European Platform. The dinocyst complex of the Mezhigorje Formation (Perkovsky *et al.* 2003*b*) contains species characteristic of the Early Oligocene zonal assemblages, *Phthanoperidinium amoenum–Wetzeliella symmetrica–W. gochtii*. This corresponds with the dinoflora characteristic of the Mezhigorian Regio-Stage of the stratotype, the Borysthen Formation of the Black Sea depression, the *Planorbella* Beds of the Crimea, the Pshekhian Regio-Stage of the Northern Caucasus, and the Rupelian Stage of Western Europe.

As for the origin of amber from Ukrainian Polesye (Rovno amber), a hypothesis regarding its large-scale transport from elsewhere has been considered for some time. During the Late Eocene and Early Oligocene, the territory between north-western Europe and the southern Urals (the so-called Subparatethys Sedimentation Province) is known to have been covered by marine basins. However, the analysis of palaeogeographic and palaeosedimentary conditions during that time interval in the north-western part of the Ukrainian Crystalline Rock Massif, permits consideration of the amber from Ukrainian Polesye as autochthonous. An indirect confirmation of this is the Eocene age of the autochthonous amber from the Lublin province in Poland (Kasinski & Tolkanowicz

1999), inferred from the amber-bearing deposits in Parchev, belonging to nannoplankton zones NP17–18 (Kosmowska-Ceranowicz *et al.* 1990).

Since both Baltic and Rovno ambers are succinite, a key to the problem of the origin of Rovno amber appears to be in analysis of their inclusions, as was predicted earlier (Zherikhin & Eskov 1999). For a long time, Rovno amber has been considered very poor in inclusions, even in comparison with Belorussian amber (Zherikhin & Eskov 1999). This was one of the main arguments against Rovno amber being autochthonous (Kosmowska-Ceranowicz *et al.* 1990). In fact, inclusions were simply destroyed or could not be used for research until the beginning of their purposeful selection at the "UkrAmber" factory (Rovno) by A. Vlaskin and E. Perkovsky for the Schmalhausen Institute of Zoology. For instance, one of the selected amber pieces weighing 30 gr (no. UA-662) was found to contain over 50 inclusions (Fig. 1).

Identification of the first hundred arthropods from the Rovno amber at the Arthropoda Laboratory indicated the peculiarity of its fauna. This was evident in the share of particular higher taxa in the assemblage, and by its species- and, sometimes, genus-level composition. Subsequent research has confirmed these preliminary results (Kasparyan 2001; Semenov *et al.* 2001; Simutnik 2001, 2002; Dlussky 2002; Dlussky & Perkovsky 2002; Kononova 2003; Perkovsky *et al.* 2003*b*; Putshkov & Popov 2003; Fedotova & Perkovsky 2004, 2005; Perkovsky & Fedotova 2004; Polilov & Perkovsky 2004; Popov 2004; Engel & Perkovsky 2006). By 2004, over 2300 pieces of Rovno amber with inclusions have been examined by the authors. The majority of pieces (2200) constitute the collection of the Schmalhausen Institute of Zoology, displaying 107 families of 19 insect orders (further referred to as Total Kiev Coll.).

Methodical selection of inclusions in Rovno amber began in 2000 at the factory "UkrAmber". After having been mined, Rovno amber, like Baltic, is sorted into size fractions (depending on the weight of specimens). The amber with layered structure is sorted separately, based mainly on its lamination and visible internal pollution, irrespective of the weight of pieces. It is worth pointing out that unlike Baltic amber, the Rovno amber is covered by a 2 mm thick oxidised crust, which often makes identification of the type of amber difficult. In our and Weitschat's (pers. comm., 2002) opinions, the thick oxidised crust of the Rovno amber, especially from Klesov, does not agree with the hypothesis regarding its long transportation, which would have resulted in considerable abrasion of the amber surface.

All inclusions in the collection were selected from translucent amber weighing 2–50 g, sourced from 120 kg of amber with a layered structure (with turbid, strongly polluted and foamy amber being excluded). These pieces were not sorted for or against any kinds of inclusion. All selected inclusions of total weight 12.3 kg were bought by the Schmalhausen Institute of Zoology in 2001–2002.

In total, the representative collection comprises 1256 remains of Arthropoda (993 insects *s.l.*, i.e. including Enthognatha) further referred to as the Representative Rovno Coll. The composition of orders, in comparison with other representative collections, is shown in Table 1. Besides succinite, a light-yellow easily melted piece of fossil resin weighing 30 g was found within layered Rovno amber, bearing seven inclusions of Chironomidae (Perkovsky & Vlaskin 2004). Together with this find, the total number of inclusions of Arthropoda recorded in 12.3 kg of amber with layered structure is 1263 (not including Diptera eggs). Table 2 shows a detailed composition of inclusions in

comparison with the Baltic representative collection of 1993. The latter collection contains 757 inclusions (519 insects *s.l.*) and is currently housed at the Booth Museum of Natural History (Brighton, England) further referred to as the Brighton Coll.

DISCUSSION

The correlation of taxonomic groups of Arthropoda in different samples of Baltic amber

Noticeable differences in inclusion composition in various collections of Baltic amber are widely known. This is usually accounted for by a biased representation (premeditated or unpremeditated preferential selection of one type of fossils and/or rejection of the others; Sontag 2003; Zherikhin & Eskov, in press). Sontag (2003), quoting relevant data on the biggest European collections—Zoological Museum in Copenhagen (Larsson 1978), Museum of the Earth in Warsaw (Kulicka 1990), Klebs Coll. (Klebs 1910) and Sontag Coll.—presented a possible explanation for these differences. In her opinion (Sontag 2003: 434), the main reason for differences in data among the authors mentioned, including her own, is, in the first two cases, the "influence of collector selection, resulting in low numbers of small arthropods such as Acari or Collembola, but in higher numbers of large Hymenoptera or Coleoptera"; and in the third case, the imperfection of optics used at the beginning of the 20th century. These are precisely the facts that explain, for instance, an abnormaly low rate of small Acari in Klebs Coll. Although this explanation appears to be logical, it is not necessarily an exhaustive one.

To explain these differences, one should consider at least three groups of factors. These include the influence of the quality of the instruments used, mentioned by Sontag (2003) (in our opinion, expertise of collectors and their working conditions in general); heterogeneity of the raw amber material, pointed out by Zherikhin (fossils from different parts of run-off area can be buried together); and the different fossil assemblages in pieces of different size (Zherikhin & Eskov, in press). Additional sources of uncertainty could include the highly seasonal occurrence of some groups like Chironomidae and aggregations of some other groups, e.g. the mite "*Acarus*" *rhombeus* Koch & Berendt and the pennicillate millipede *Polyxenus* Goldfuss.

The importance of differences in origin of various samples of Baltic amber is also beyond doubt. But there is insufficient data available to substantiate this hypothesis. In order to gain some perspective on the origin of Baltic samples, it would be beneficial to compare the composition of assemblages from Yantarny and the northern coast of the Jutland. Unfortunately, the Danish representative collection is not yet available for study. However, a comparative analysis of the ant composition in Danish and other Baltic samples, is currently in progress (G.M. Dlussky pers. comm., 2005). An analysis of the influence of the size of amber pieces will have to be postponed until Zherikhin and Eskov's article is published.

Comparative study of Baltic and Rovno amber

The problems discussed above favour cautious consideration in dealing with relationships between Baltic and Rovno amber. This includes questions as to whether or not these two amber types had the same origin; whether they came from different parts of the same river basin, or whether they originated from entirely different basins within the same continental mass.

TABLE 3

Composition of ants (Formicidae) in representative samples of Baltic amber (Brighton Coll.) and Rovno amber (Representative Rovno Coll.); subfamilies of ants and respective figures are given in bold. Fossils not identified with confidence are considered in totals even if not shown in the table.

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Dolichoderinae	**14**	**63.6**	**16**	**43.2**
Ctenobethylus goepperti (Mayr)	13	59.1	11	29.7
Iridomyrmex geinitzi Mayr	–		1	
Dolichoderus polessus Dlussky	–		1	
Dolichoderus sp. n.	–		1	
Formicinae	**8**	**36.4**	**11**	**29.7**
Camponotus mengei Mayr	1		–	
Formica flori Mayr	1		1	
Lasius schiefferdeckeri Mayr	4	18.2	6	16.2
Plagiolepis minutissima Dlussky	–		2	
Prenolepis henschei Mayr	1		–	
Myrmicinae	**–**		**6**	**16.2**
Aphaenogaster antiqua Dlussky	–		1	
Oligomyrmex nitidus Dlussky	–		1	
Oligomyrmex ucrainicus Dlussky	–		1	
Leptothorax sp.	–		1	
Myrmicinae gen. et sp. n.	–		2	
Ponerinae	**–**		**1**	**2.7**
Gnamptogenys europaea (Mayr)	–		1	
Pseudomyrmecinae	**–**		**1**	**2.7**
Tetraponera simplex (Mayr)	–		1	
Formicidae indet.	**–**		**2**	**5.4**
TOTAL	22	100	37	100

The general faunal composition of Rovno amber at the level of taxa of the highest rank (Table 1) gives definite, but not necessarily reliable, evidence, making it distinct from Baltic amber. This is supported by the essentially lower number of Aphidinea and Acari, in comparison with any of the representative samples of Baltic amber which has been analysed. The reliable, distinguishing features of the Rovno and Baltic amber faunas at the species level (e.g. Formicidae) allow us to make preliminary conclusions as to the differences in faunal origins of Rovno and Baltic amber, i.e. it is most likely that they were formed in different areas of Late Eocene Europe.

Dlussky and Perkovsky (2002) showed that Rovno amber contains an extremely high number of new species (26% of all identifiable specimens). New Baltic amber collections of the same volume have only 2–5% of new species. In Rovno amber, Dlussky described five new species of Dolichoderinae (Dlussky 2002; Dlussky & Perkovsky 2002), one species of Formicinae and three species of Myrmicinae (Dlussky & Perkovsky 2002). Four new species and one new genus are yet to be described (Dlussky, pers. comm.).

Worth mentioning is the difference in representation of the main Formicidae subfamilies (Table 3). The figures given by Dlussky and Perkovsky (2002) for the ants from Representative Rovno Coll. need to be corrected, because six specimens do not belong to Representative Rovno Coll. and were included in the calculations by mistake. The corrected figures are as follows: Representative Rovno Coll. contains noticeably fewer Dolichoderinae (43% vs. 64% in Brighton Coll.), and the number of Myrmicinae

is, on the contrary, increased (16% vs. nil). At least 9 of 37 specimens belong to new species and genera unknown in Baltic amber.

Similarly, upon examination of 41 Rovno amber spiders, Wunderlich (2004) described or indicated a number of taxa never recorded in the amber of Samland origin, viz. *Balticonopsis perkovskyi* Wunderlich, *Fossilanapis* sp. indet., Anapidae indet., *Succinero rovnoensis* Wunderlich and *Gorgopsina fractura* Wunderlich. The families Anapidae, Mimetidae and Salticidae are, however, well studied in Samlandic amber. A quarter of the adult male spiders (Aranei) from Rovno amber belong to new species. All gall-midges from the Representative Rovno Coll., which have been identified to the species level (including *Campylomyza superposita* Fedotova and *Didimomyia accidentalis* Fedotova (Fedotova & Perkovsky 2004, 2005)) are found to be unknown in the Baltic amber.

The comparison of arthropod composition, identified in the more thoroughly studied collections (Representative Rovno Coll. and Brighton Coll.; Table 2), reveals additional, and in some cases significant, differences. The Representative Rovno Coll. contains almost half as many Homoptera (4.8% vs. 8.6%) (6.8% of insects *s.str.* in Sontag Coll.) and rather many Collembola (6.9% vs. 5.6%; 7.8% in Sontag Coll.). The abundance of Collembola, in particular, does not allow us to explain the small number of Acari by assuming that Rovno amber is poor in small arthropod inclusions. Under-representation of mites (Acari) in the Representative Rovno Coll. (15.8% vs. 27.0%; 24% in Sontag Coll.) is due to the relative scarcity of "*Acarus*" *rhombeus*: 31.3% in Representative Rovno Coll. vs. 56.9% of all mites in the Brighton Coll. The majority (65%) of *A. rhombeus* in the Representative Rovno Coll. have been found in two pieces of amber, one containing *Machilis*, and the other containing cockroaches. The origin of these amber pieces may have been associated with a relatively wetter habitat. In the Brighton Coll., two pieces, which are richest in this species, produce only 33.6% of all *A. rhombeus* in the sample. The rest of the mites together constitute 10.8% of all arthropods (11.3% of all arthropods identified to the order level) in the Representative Rovno Coll., and 11.6% (11.8% of all arthropods identified to the order level) in the Brighton Coll.

Among the Collembola of the Representative Rovno Coll., the Entomobryidae are more dominant than in the Brighton Coll. (Table 2). Out of 139 Collembola of the Total Kiev Coll. identified to families, 59.7% are Entomobryidae and 24.5% are Sminthuridae. The collembolan assemblage would seem to indicate that the climate of the Rovno amber forest was relatively dry.

The decreasing number of Homoptera in Rovno amber results primarily from the low representation of *Germaraphis* aphids: this genus accounts for 65.9% of Homoptera (5.7% of all insects) in the Brighton Coll. versus 23.4% (1.1% of all insects) in the Representative Rovno Coll. (Table 2). Rovno amber (Representative Rovno Coll.) contains noticeably fewer scale insects: their proportion among all insects (0.66%) is 2.6 times that in the Brighton Coll. (1.68%; 1.69% in Sontag Coll.). Only two small larvae of *Germaraphis* constitute a part of a syninclusion in the Representative Rovno Coll., while in the Brighton Coll., the syninclusions, containing more than one specimen of *Germaraphis,* account for 55.6% of all *Germaraphis*. The proportion of Auchenorrhyncha among Homoptera in the Representative Rovno Coll. is much higher – 26.1% vs. 4.9% (10.1% in Sontag Coll.).

The dipteran proportion in the Representative Rovno Coll. is similar to that in the Brighton Coll. – 69.3% vs. 71.7% (67.3% in Sontag Coll., 72.1% in Hoffeins Baltic

TABLE 4

Composition of Diptera in the representative samples of Baltic (Brighton Coll., Sontag Coll., Hoffeins Baltic Coll.), Bitterfeld (Hoffeins Bitterfeld Coll.) and Rovno (Representative Rovno Coll.) amber. Fossils incertae sedis are not counted; numbers of Empididae *s.l.* and Tipuloidea in the Sontag Coll. are considered unknown, because Sontag (2003) did not specify if she included Hybotidae, Microphoridae and Tipulidae under the above names, or separately. In Sontag Coll., Mycetophilidae are given under Mycetophilidae *s.l.*, otherwise Mycetophilidae *s.l.* are Mycetophilidae + Keroplatidae. Tipuloidea means Tipulidae + Limoniidae.

Family	Brighton Coll.	Sontag Col.	Hoffeins. Baltic Coll.	Hoffeins Bittereld Coll.	Representative Rovno Coll.
Chironomidae	139 (42.2%)	1141 (42.2%)	1376 (37.5%)	2410 (33.9%)	137 (22.9%)
Sciaridae	52 (15.8%)	506 (18.7%)	728 (19.9%)	1562 (22.0%)	189 (31.6%)
Mycetophilidae *s.l.*	24 (7.3%)	230 (8.5%)	317 (8.6%)	795 (11.2%)	55 (9.2%)
Ceratopogonidae	20 (6.1%)	158 (5.9%)	224 (6.1%)	459 (6.5%)	29 (4.8%)
Cecidomyiidae	24 (7.3%)	114 (4.2%)	105 (2.9%)	202 (2.8%)	23 (3.8%)
Psychodidae	6 (1.8%)	89 (3.3%)	90 (2.5%)	109 (1.5%)	16 (2.7%)
Tipuloidea	5 (1.5%)	–	78 (2.1%)	123 (1.7%)	51 (8.5%)
Scatopsidae	–	3 (0.1%)	3 (0.1%)	14 (0.2%)	3 (0.5%)
Ptychopteridae?	1 (0.3%)	–	–	–	–
Simuliidae	1 (0.3%)	2 (0.1%)	1	6 (0.1%)	–
Mycetobiidae	–	1	3 (0.1%)	1	1 (0.2%)
Dixidae	–	–	1	2	–
Bibionidae	–	–	2	–	–
Nymphomyiidae	–	–	1	1	–
Corethrellidae	–	–	0	1	–
Dolichopodidae	38 (11.6%)	271 (10.0%)	486 (13.3%)	865 (12.2%)	64 (10.7%)
Phoridae	3 (0.9%)	65 (2.4%)	117 (3.2%)	328 (4.6%)	18 (3.0%)
Empididae *s.l.*	13 (4.0%)	–	110 (3.0%)	176 (2.5%)	7 (1.2%)
Rhagionidae	–	8 (0.3%)	12 (0.3%)	18 (0.3%)	4 (0.7%)
Syrphidae	2 (0.6%)	2 (0.1%)	3 (0.1%)	5 (0.1%)	–
Athericidae	–	–	–	2	–
Bombyliidae	–	–	1	0	1 (0.2%)
Opetiidae	–	–	1	0	–
Drosophilidae?	–	1	–	–	–
Xylomyidae	–	–	0	1	–
Acalyptrata	–	–	8 (0.2%)	31 (0.4%)	–
Anthomyiidae?	1 (0.3%)	–	–	–	–
TOTAL	329	2702	3667	7111	598

Coll.) of insects *s.str.* Within the order (Table 4), the Representative Rovno Coll. contains half as many Chironomidae (22.9% vs., respectively, 42.2%, 42.2% and 37.5%); almost twice as many Sciaridae (32% vs. 16%; 19%, 20%); and 6.8 times as many Limoniidae (6.1% vs. 0.9% Brighton Coll. and 1.9% in Sontag Coll.). The proportion of Dolichopodidae is the same as in the Brighton Coll., that of Empididae *s.l.* is less (1.2% vs. 4.0%; 3.0% – in Hoffeins Baltic Coll.); while the proportion of Phoridae is more (3% vs. 0.9%; 2.4% in Sontag Coll.; 3.2% – in Hoffeins Baltic Coll.).

The Representative Rovno Coll. shows a deficiency of aquatic and subaquatic dipterans, particularly Chironomidae, while the number of families connected with leaf litter ("*Sciara* zone" according to Larsson 1978), such as Sciaridae, Limoniidae, Tipulidae, Psychodidae, Phoridae, Mycetophilidae and Keroplatidae is twice that in Brighton Coll. (55% vs. 27%) (Table 4). This conclusion is further supported by the fact that in the Rovno amber, there are many forms connected with leaf litter, even among the Chironomidae.

The Rovno amber fauna also shows a deficiency of hygro- and hydrophilous Coleoptera. Baltic amber collections contain 14–23% Helodidae (Klebs 1910; Hieke &

Pietrzeniuk 1984), while in the Total Kiev Coll., they account for only 7% out of 200 beetles. On the contrary, leaf-litter forms of the "*Sciara* zone", particularly Staphylinidae, Scydmaenidae, Leiodidae (Leiodidae from the Rovno amber can also be referred to the "*Sciara* zone") and Ptiliidae are abundant. Staphylinoids are extremely numerous and account for 23% of all beetles. Ptiliids account for 4.6% of all Representative Rovno Coll. beetles (not 3.5%, as was erroneously mentioned by Polilov & Perkovsky 2004). They are represented by two specimens of *Ptilium* (found in one piece of amber) and by the holotype of *Ptinella rovnoensis* Polilov & Perkovsky.

Among hymenopterans, the proportion of ants is almost the same in both collections – 43% vs. 44% (49.8% in Sontag Coll.). In the Total Kiev Coll. (3600 inclusions, 2735 insects), ants account for 6% of all insects (not 7.6% as given by Dlussky & Rasnitsyn 2003) (5.8% in Sontag Coll.). Worth mentioning is the higher abundance of myrmicine and lower abundance of *Ctenobethylus goepperti* (Mayr) in the Representative Rovno Coll. (*C. goepperti* represents 29.7% of all ants vs. 59.1% in the Brighton Coll.; Table 3). There are no pieces of amber containing more than one specimen of *C. goepperti* in the Representative Rovno Coll., while in the Brighton Coll. 46.2% of *C. goepperti* are found in such syninclusions. In addition, other hymenopterans show obvious differences: there are three times as many Scelionidae in the Representative Rovno Coll. (18.4 vs. 6%), while Diapriidae are less numerous (9.2% vs. 12%) (Table 2). Other families of hymenopterans are too few in number to justify comparison (the larger number of ichneumonids, compared with braconids in the Brighton Coll., is undoubtedly a sample bias). The same holds true for the other arthropod groups, which are represented in the examined collection, but are not included in the comparisons.

CONCLUSIONS

A comparison of the representative samples of the Baltic and Rovno amber points toward independent origins of their respective faunas. The differences observed are in part indicative of their ecological nature. For instance, compared to the Baltic assemblage, the Rovno amber is distinctly impoverished in aquatic and coastal arthropods while enriched with the leaf-litter dwellers of the "*Sciara* zone". Rarity of aphids in the Rovno amber suggests a warmer, possibly subtropical climate of the Ukraine Crystalline Rock Massif in the Late Eocene, while a higher number of Scelionidae in the Rovno assemblage is indicative of a more xeric environment, This is in contrast to the Baltic amber, where Diapriidae are more abundant.

The age of the Baltic amber and stratigraphic correlation of the amber-bearing Prussian Formation are considered in some detail. It is concluded that proposal of a Middle Eocene (Ypresian–Lutetian) age contradicts a wide array of the palaeontological, radiological, and stratigraphic data and thus cannot be accepted on the basis of available evidence.

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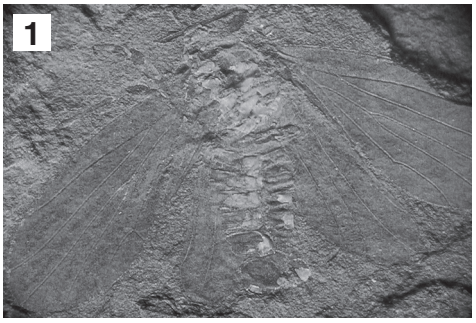
NOTES AND COMMENTS

New insect discoveries at the Upper Jurassic Talbragar fish beds, New South Wales, Australia

Cicada lowei Etheridge & Oliff, 1890 is the only described insect fossil from the Talbragar fish beds. A poorly preserved insect was discovered in 1975, and approximately 60 specimens were collected in 1995 by Steven Avery, 42 of which were donated to the Australian Museum in Sydney. The remaining specimens were passed to me for study, prior to donation to the Museum. A survey of the beds in April and October 2006 yielded another 28 specimens, as well as numerous examples of insect-plant interactions in a form of damages to *Pentoxylon australica*.

The entire entomofauna, as yet undescribed, consists largely of protopsyllids (Fig. 1), with a smaller proportion of beetles (Fig. 2), two specimens provisionally ascribed to Neuroptera, and one tettigonid specimen. The entomofauna is associated with a rich assemblage of early teleost and palaeoniscid fish as well as coniferous plants. Most of the specimens are complete in contrast to those from the Upper Permian locality of Belmont. This prompts further investigation, since the deposition environments of both localities were similar and involved volcanic ash fall.



Figs 1, 2. Newly discovered insects from the Talbragar beds: (1) Protopsyllid, dorso-ventral view; (2) Beetle, dorsal view.

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IGCP 469 – Late Variscan terrestrial biotas and palaeoenvironments

This international project is concerned with biotic and environmental change across the Westphalian/Stephanian transition during the Pennsylvanian. Many of the changes are linked to the Variscan (Hercynian) Orogeny, which had an impact on the coal-forming swamp vegetation and associated fauna.

Mid-late Upper Carboniferous insect faunas are less well documented than the plants but include classical sites and collecting areas in Euramerica (USA, UK, France, Germany, Czech Republic and Russia). Other areas are less well studied (Canada, Poland) or relatively unknown (Bulgaria, the Ukraine) and with potential beyond the orogen (China). The insects include diverse palaeopterans and polyneopterans, some with well-developed colour patterns (Jarzembowski 2005). They are associated with other invertebrates and some vertebrates, and preserved in sideritic nodules or roof shales. The latter have yielded a sizeable assemblage in the late Asturian ('Westphalian D') of Writhlington (Somerset Coalfield) in the Variscan Foreland of southern England (Jarzembowski 2004). Cockroachoids (Blattodea) are sufficiently abundant (especially around the transition) to assist with biostratigraphy (Jarzembowski & Schneider, in press). New work on insects is in progress in the USA (Cary Easterday; http://groups.yahoo.com/group/paleogeoarthropoda/), the UK (Prokop *et al*. 2006) and the Czech Republic (Prokop & Nel 2004, 2007). Site geoconservation is also needed especially in former coal-mining areas, which are liable to redevelopment with attendant loss of geology. An old colliery tip ('sterile dump') has recently yielded the first Pennsylvanian insect from Romania showing the potential for more collecting (Jarzembowski, in press).

Project meetings are held in participating countries and future ones include Birmingham (22–26 April 2007). For further information, consult the Project newsletter at http://www.palaeobotany.org/modules.php?name=iop&sec=meetings&page=40 or http://www.nmgw.ac.uk/www.php/301/ .

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EDNA The world-wide fossil insect catalogue

EDNA aims to catalogue all the known fossil insects that have been named as a fossil (Mitchell 2003). It therefore does not include extant species that have been found in the fossil record. Also recorded is the author and full reference, the taxonomic hierarchy from subfamily to order, the site and formation in which the holotype was found and the geological age. Synonyms are also recorded along with the reference to where the change was noted.

To date (22 March 2007), 23 210 species including 3414 synonyms are recorded from 3917 references. They come from 1485 sites and 1691 families.

Handlirsch's monograph (1906–08), has been taken as a starting place. Assuming, rightly or wrongly, that he had found all the known references, those prior to 1890 have not been checked for accuracy.

Because of translation problems it has sometimes been difficult to find the exact site, formation and geological ages for some species, but this problem is slowly being resolved. There are also some occasions when mention has been made of a new species, which is probably a fossil, but where no reference is given. These species have been added to the database but without other details. On other occasions a reference is given but seems to be incorrect. The correct reference to many of these 'orphan' species is slowly being resolved.

EDNA is recorded in Microsoft Access 2000 so that anyone with the Microsoft Office suite of programmes can use it. There are several basic searches built in, such as listing all species in a particular family, suborder, order etc.; publications or species by a particular author, or species by site, formation or geological time. There is also basic instruction for making tailor-made queries to search for a combination of categories, e.g. Cretaceous Hymenoptera from Australia, and displaying only those pieces of data required. For more detail on the data recorded see Mitchell (2003).

EDNA should soon be completed as far as it is possible and work is in progress to publish the whole database on the web; it will also be available on a CD. The final version could include the facility to add more data and produce site-based species lists. A test version with 16 000 species is currently available on CD.

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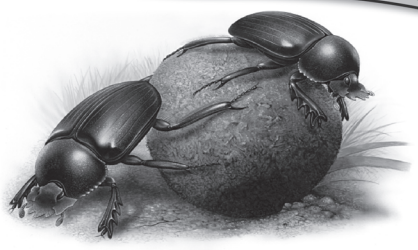

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The Natal Museum had its origins in the Natal Society (founded in 1851), and was established in 1903 by the Government of Natal. Since 1910 it has been one of the National Museums of South Africa. The Museum has extensive exhibition galleries (and associated study collections) devoted to the archaeology, anthropology, cultural history, geology, palaeontology and zoology of South Africa, with special emphasis on the Province of KwaZulu-Natal. There are two Natural Science divisions currently active, both of which concentrate on the study of the systematics and biology of invertebrates.

- The **Division of Arthropoda** includes the Lawrence and Stuckenberg collections. The Lawrence collection dates to the foundation of the Museum and includes extensive holdings of southern African Arachnida, Onychophora and Myriapoda. The Stuckenberg collection of Diptera is the largest and most diverse in Africa; founded in 1953 it includes the older collections of the Transvaal Museum and the Zumpt Collection of the South African Institute for Medical Research. The Department also supervises collections management activities for the natural sciences, and is responsible for the curation of the extensive J. D. Plisko collection of South African Oligochaeta. This is the largest and best documented collection of earthworms in Africa.
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